Université Paris-Sud

Ecole Doctorale : Sciences du Végétal

Laboratoire Ecologie, Systématique, Evolution
UMR 8079, Université Paris-Sud, CNRS, AgroParisTech

Discipline : Biologie

Thèse de doctorat

Soutenue le 17 Juin 2015 par

Joannès GUILLEMOT

Productivity and carbon allocation in European forests: a process-based modelling approach

Etude de la productivité et de l'allocation du carbone des forêts européennes : une approche basée sur la modélisation des processus

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Composition du jury :		
Présidente du jury :	Claire Damesin	Professeur (Université Paris-Sud)
Rapporteurs :	Annikki Mäkelä	Professor (University of Helsinki)
	Sönke Zaehle	Scientist (Max Planck Institute for Biogeochemistry)
Examinateurs :	Guerric le Maire	Chercheur (CIRAD)
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Chapter 1

General introduction

1. Forests and the global carbon cycling

Forests cover ~42 million km^2 worldwide, amounting to a third of the land surface (Bonan, 2008) and are estimated to contain 40% of the terrestrial biomass (Sabine et al., 2004), i.e., 861±66 PgC (Pan et al., 2011). Inventory-based studies show that in the recent decades, forests have been a persistent carbon (C) sink (Brienen et al., 2015), uptaking 2.4±0.4 PgC $year^{-1}$ in existing forests (Pan et al., 2011). The net C sequestration in forests from 1990 to 2007 has been 1.1±0.8 PgC $year^{-1}$ (Pan et al., 2011), which corresponds to a third of the anthropogenic C emissions and accounts for most of the terrestrial C sink, even though non-forest contribution may have been under-estimated thus far (Liu et al., 2015). In a context of increasing fossil fuel emissions (+65% between 1990 and 2014, Le Quéré et al. (2014)), forests therefore contribute to reduce the airborne fraction of anthropogenic CO_2, thus mitigating climate change (Shevliakova et al., 2013).

Both mass balance analyses and modelling studies show that the global land C sink has been increasing over the past 50 years (Ballantyne et al., 2012; Sarmiento et al., 2010). These observations are consistent with the enhancement of forest wood growth observed in several regions of the world over the same period (Ciais et al., 2008; Fang et al., 2014; McMahon et al., 2010; Pretzsch et al., 2014). The increase in forest productivity and C sequestration has been attributed to the alleviation of a number of environmental limitations: (1) the increase of global photosynthesis caused by CO_2 fertilization (Drake et al., 2011b; Keenan et al., 2011; Leakey et al., 2009; Norby et al., 2005), (2) nitrogen depositions (Fernández-Martínez et al., 2014; Janssens and Luyssaert, 2009; Magnani et al., 2007) that may increase the ecosystem apparent photosynthetic capacity (Fleischer et al., 2013), change tree C allocation from fine roots to shoot biomass (Smithwick et al., 2013) or reduce the forest soil respiration (Janssens et al., 2010); and (3) the increase of the leafy period that is induced by climate warming (Barichivich et al., 2013; Dragoni et al., 2011; Keenan et al., 2014). However, results from FACE experiments suggest that these fertilization effects on forest productivity may not be persistent in the future, mostly because of the interactions between limiting environmental factors (Körner et al., 2005; Leuzinger et al., 2011; Norby et al., 2010), that include progressive limitations by nutrients, such as nitrogen (Luo et al., 2004), phosphorus (Vitousek et al., 2010) or potassium (Sardans and Peñuelas, 2015). In addition, the increasing aridity induced by climate change over large areas (Dai, 2011) may negatively affect forest productivity and terrestrial C sink. The heatwave

that occurred over Europe in 2003 changed the European forests from C sink to C source (Ciais et al., 2005), and a number of local and regional studies report declines in forest wood growth that may be linked to drought (Brienen et al., 2015; Jump et al., 2006; Lévesque et al., 2014; Nabuurs et al., 2013). Drought also play a predominant role in the forest diebacks occurring worldwide (Allen et al., 2010; Brienen et al., 2015; Carnicer et al., 2011), with potential effects on the future global C cycle (Anderegg et al., 2013). Finally, the increasing aridity is likely linked to the increasing of forest disturbances (Bond-Lamberty et al., 2007; Seidl et al., 2014) such as wildfires and bark beetles outbreaks, which are responsible for massive CO_2 releases in the atmosphere (Prentice et al., 2011).

Additionally to the changes in forest productivity, the future of the terrestrial C sink may be affected by changes in the allocation of C among the tree compartments (within-tree C cycling). Carbon allocation is key in our understanding of the outcome of global changes on forests because it determines the fraction of C that is sequestered in woody biomass for decades (Zhang et al., 2010). Experimental studies revealed that the fluctuations of annual wood growth in forest trees not only reflect changes in productivity, but also shifts in C allocation (Campioli et al., 2011; Doughty et al., 2014, 2015; Rambal et al., 2014). Biometric data are very common in forest science, but are most of the time confined to stand biomass estimations (Litton et al., 2007). Such data do not give a direct access to annual C stand growth and allocation (Doughty et al., 2014). Tree growth data are therefore needed to increase our understanding of the allocation of C at the whole plant level and evaluate the future of tree C allocation in the face of global changes. The potential increase of soil C cycling in a CO_2-enriched atmosphere may be of major importance in the long run (Finzi et al., 2014; Leuzinger and Hättenschwiler, 2013): increased fine root turn-over and allocation to root symbiont (Iversen et al., 2008; Jackson et al., 2009) may either increase C storage in long-lived soil pools or enhance microbial decomposition and CO_2 efflux (van Groenigen et al., 2014; Langley et al., 2009). The long-term effect of C allocation change on soil C storage, which may contains up to three times as much C as the Earth's atmosphere (Sabine et al., 2004), is therefore still unclear.

Apart from the environmental control of forest productivity and C allocation, the human impact on forest functioning and species distributions, which affects all biomes (Fig. 1), has a significant effect on the forest C balance of large areas.

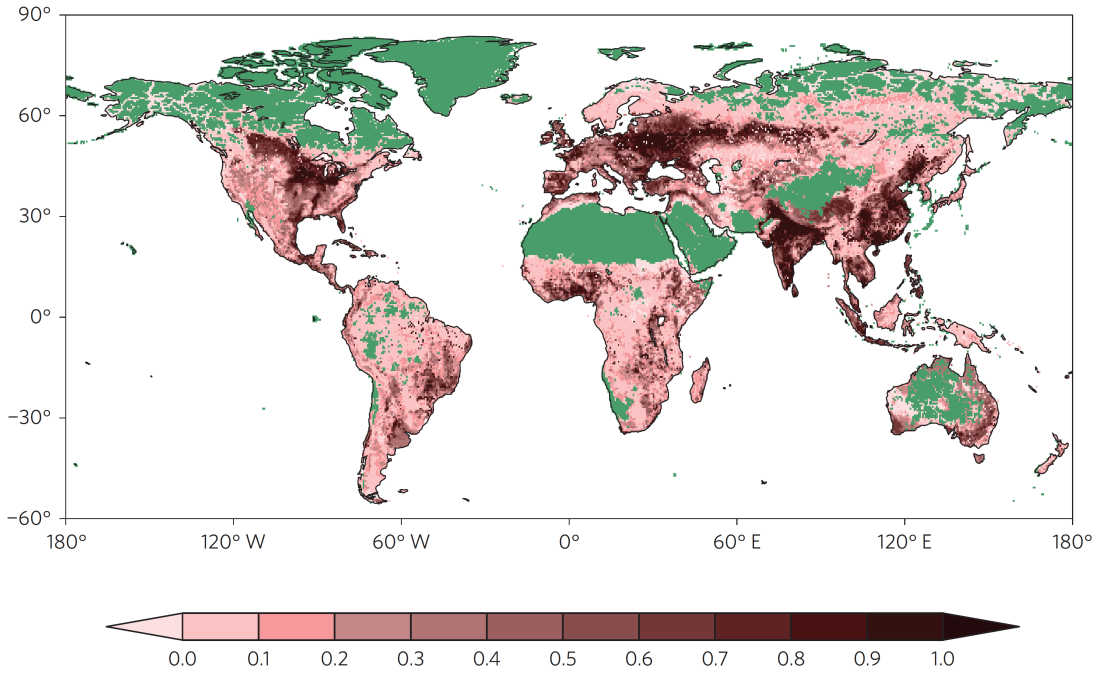

Figure 1: Spatial extent of land cover change, land management, wilderness and non-productive areas. Wilderness and non-productive areas are shown in green and represent land largely unaltered by humans. The remaining land is used for producing food, fibre and fuels, and for hosting infrastructure. The colour scale represents the fraction of each grid cell for which the original plant cover was converted. Dark colours indicate regions where most of the original plant cover was converted; these regions are the subject of typical land cover change studies. The light colours show areas for which land cover change is low, but which are nevertheless under anthropogenic land management. (**Figure from Luyssaert et al. (2014)**).

The most striking example are probably the tropical forests: although models show that the tropics should have been the most important C sink in the last decades (Sitch et al., 2015), deforestation turned it into a net C source (Pan et al., 2011). Although the effect of land use changes on the terrestrial C sink (Houghton et al., 2012; Zaehle et al., 2007) and the species distributions (Appendix A3, Hanewinkel et al., 2012; Thuiller et al., 2004) received considerable attention, less effort was dedicated to changes in forest management, which may also have substantial effects on the atmospheric CO_2 concentration (Hudiburg et al., 2011, 2013) and climate (Luyssaert et al., 2014; Otto et al., 2014). For example, the important European C sink during the second part of the 20^{th} century (Luyssaert et al., 2010) has partly been attributed to both a bias of the managed European forests towards young age-classes and to a progressive decrease of wood harvests (Ciais et al., 2008; Nabuurs et al., 2013). Another important aspect regarding the link between forest management and global C budget is the use of forest for producing bioenergy, which has the potential to reduce the fuel C emission (Hudiburg et al., 2011). On the basis of these elements, forest management is considered as an important tool for

the mitigation of climate change (Canadell and Schulze, 2014).

2. Forest productivity and carbon allocation

The interplay between forest productivity and C allocation is an important research topic (Doughty et al., 2015). Current knowledge suggests that the different meristems that are responsible for the growth of the tree organs have specific environmental and internal controls (Delpierre et al., 2015[1]; Schiestl-Aalto et al., 2015). This point is illustrated in Fig. 2 with the example of the Morgan-Monroe State Forest where a divergence between the trends of leafy and wood growth period durations has been established (Brzostek et al., 2014).

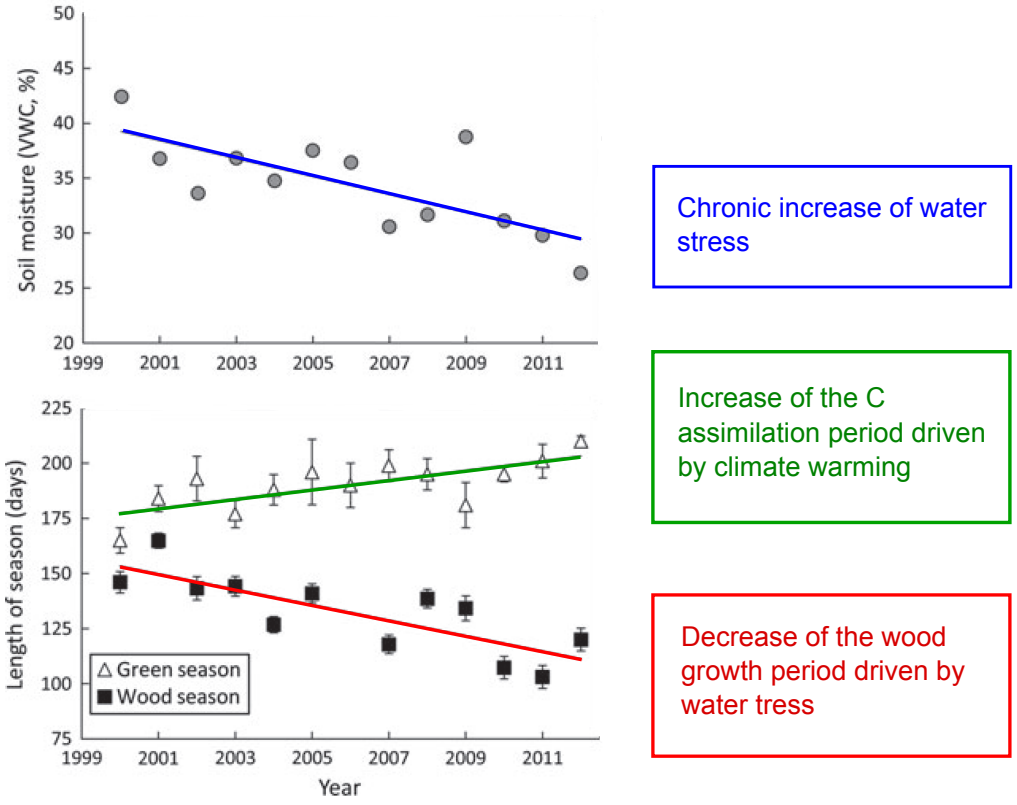

Figure 2: Decade-long changes in phenology are tracked by decreases in water availability at the Morgan Monroe State Forest. Volumetric water content (VWC, top plot) in the upper 15 cm of soil (n = 13; $R^2 = 0.53$; P < 0.005). Concurrent with declining water availability, the length of foliar season increased (bottom plot, n = 13; $R^2 = 0.53$; P < 0.005), whereas the length of the wood season decreased (bottom plot, n = 12; $R^2 = 0.64$; P < 0.002). Error bars in the top plot are too small to be visible. (**Figure adapted from Brzostek et al. (2014)**).

This resulted in a decoupling of the annual wood growth and annual C assimilation: water stress at this site appears to affect differently wood growth and C assimilation. This observation

[1]This article is provided as part of this thesis in Appendix A2.

is consistent with results from other studies (Gea-Izquierdo et al., 2015; Lempereur et al., 2015). The decoupling between growth and C assimilation received experimental support at the cell scale, with a number of study reporting that meristem activities are more sensitive than C assimilation to several environmental stressors. In particular, the decrease in cell turgor that occurs because of water stress strongly affects cell division and expansion (Woodruff and Meinzer, 2011) before there is any strong reduction in the gas exchange (Muller et al., 2011; Tardieu et al., 2011). Similarly, cell division is more sensitive to a decrease in temperature than photosynthesis is, and stops at much higher temperatures (e.g. with a commonly cited limit threshold of +6°C) than photosynthesis does (Körner, 2008). These observations suggest that tree growth is more affected by the limitation of the sink activity than by the availability of the C source (Fatichi et al., 2014). The idea of a sink limitation of tree growth replaces the dynamic of C allocation at the core of the response of forest growth to environmental constraints. However, the processes underlying C allocation in trees are far from being completely known. Overall, the literature reports conflicting relationships between the C supply and wood growth at particular sites (Gielen et al., 2013; Richardson et al., 2013), ranging from non-significant (Mund et al., 2010; Richardson et al., 2013; Rocha et al., 2006) to highly significant (Babst et al., 2014; Ohtsuka et al., 2009; Peichl et al., 2010; Zweifel et al., 2010). The processes that underlie these contrasted correlative observations remain poorly understood and have not been represented in a single, mechanistic framework. More generally, it is worth considering that although wood is an important (in terms of mass) and perennial C sink, the tree primary meristems produce annually an amount of leaf, fine roots and fruit biomass that is of the same order of magnitude that the growth of woody biomass (Campioli et al., 2011; Granier et al., 2008; Rambal et al., 2014). The specific environmental and internal controls of the growth of these organs is an active research area (Delpierre et al., 2015; Génard et al., 2008; Knops et al., 2007; Schiestl-Aalto et al., 2013).

The C allocation to the tree organs, and thus their relative growths, is coordinated at the whole plant level (Delpierre et al., 2015; Franklin et al., 2012). In the absence of a mechanistic understanding of these dependences among organs, a number of assumptions have been suggested to explain the C allocation in trees (Franklin et al., 2012) and its relation to forest productivity. These hypotheses include (1) the functional homeostasis in water transport within trees, which is related to the mechanical constraints associated with plant hydraulic architecture and the construction of the water-transport system (Magnani et al., 2000). (2) functional balances, for

instance via a preferential allocation of C to the organ responsible for the acquisition of the most limiting resource (McCarthy and Enquist, 2007; McMurtrie and Wolf, 1983; Reynolds and Chen, 1996; Thornley, 1991). (3) the maximization of a tree function that is assumed to reflect fitness, for instance net growth or net primary production (optimality approaches, Dewar et al., (2009); Franklin, (2007); Mäkelä et al., (2008)). (4) the interplay between the optimal response of tree allocation and the influence of competition in a evolutionarily perspective (game theoretically based approaches, Dybzinski et al., (2011, 2014); Farrior et al., (2013)). Attempts to compare or integrate these different approaches in a common modelling framework are scarce, despite the potential benefit to highlight the limits of the different models and go beyond their respective caveats. In a promising study, Weng et al., (2014) implemented a game theoretically-based module in the LM3 process-based model (PBM), linking our knowledge of physiological processes to the hypothesized constraint of evolution on C allocation.

Finally, C allocation may interact with forest productivity through its possible role in the mortality of trees. The interaction between the C-related processes and hydraulic failure is at the core of our current understanding of the drought-induced forest dieback (Bréda et al., 2006; McDowell et al., 2011; Mcdowell et al., 2008). Hydraulic failure may indeed be associated with loss of adequate tissue carbohydrate content required for osmoregulation (Sevanto et al., 2013). The cessation of phloem transport during drought as a consequence of decreasing cell turgor seems to be a mechanism that promotes plant mortality (Sevanto, 2014), possibly because it prohibits the redistribution of carbohydrate reserves to starving tissues (McDowell and Sevanto, 2010; Sala et al., 2012). Consistently, several experimental studies reported that the C reserve pool of trees is an active sink, which may be temporarily prioritized at the expense of wood growth (Delpierre et al., 2015; Dietze et al., 2014; Gilson et al., 2014; Sala et al., 2012; Wiley et al., 2013). These results suggest that the dynamic changes of C allocation over time are plastic or evolutionary responses that promote tree and forest productivity on the long run (Wiley and Helliker, 2012). They also stress the need to understand and predict the seasonal and annual changes in C allocation, as mortality may result from a combination of long-term predisposing factor of stress and short-term extreme events leading to the passing of mortality thresholds (Bréda et al., 2006; Linares et al., 2010; Lloret et al., 2011).

3. Forest productivity and management

Forests provide a variety of ecosystem services to the humankind, including C sequestration, flood mitigation, biodiversity, food and timber production, and opportunity for recreation (Raudsepp-Hearne et al., 2010). The management of forest aims to optimizing one or several of these services, through clear cuts, partial thinning or species changes (Kangas et al., 2005). If dealing with C sequestration and productivity, we note that forest management strongly modulates (1) the amount and distribution of available growing space in a stand, and (2) the stand structure, i.e., the statistical distribution of the tree dimensions. Overall, the result is an alleviation of the competition intensity experienced by the trees (as compared to an unmanaged stand), which has been shown to change the stand growth responses to extreme events, such as drought (Gea-Izquierdo et al., 2009; Gomez-Aparicio et al., 2011; Olivar et al., 2013; Piutti and Cescatti, 1997), most likely as a consequence of increased resource availability (Bréda et al., 1995; Nambiar and Sands, 1993). The acclimation of existing forest stands to increasing drought relies on different physiological adjustments, among which leaf area reduction seems of particular importance over the long term (Martin-StPaul et al., 2013; Maseda and Fernández, 2006), and may be related to changes in stem density (Barbeta et al., 2013). Forest management, (through thinning) could thus mimic stand acclimation. For instance, a study conducted in a cedar plantation of southern France showed that the negative impact of a dry year on wood growth was significantly reduced in a heavily thinned plot, compare to moderately thinned or unthinned plots (Fig. 3, right panel, Guillemot et al., 2015a, Appendix A1).

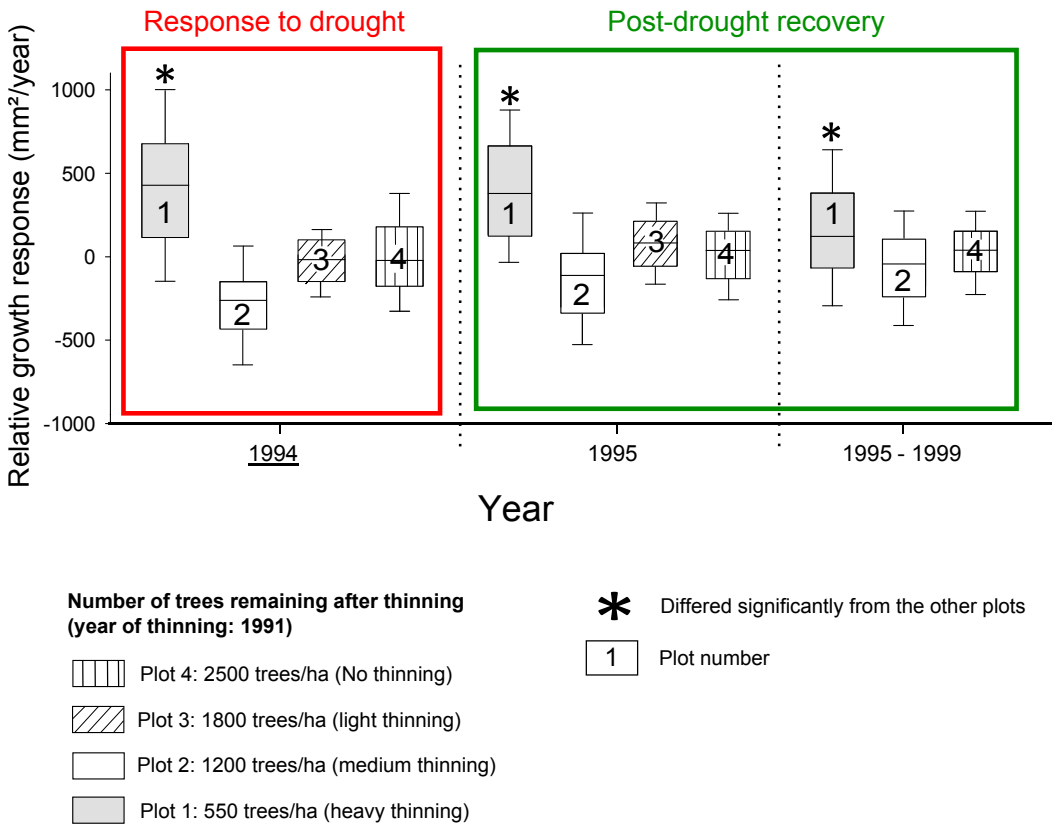

Figure 3: Growth response and recovery to the drought of 1994 in cedar plantations under contrasted management intensity. Thinning operations of contrasted intensities were conducted on plot 1 to 3 in 1991. The relative annual growth is presented for 1994 (left panel, growth response to drought), 1995 (middle panel) and for an averaged 1995-1999 post-drought period (right panel). Plots with a '*' differed significantly from the others (at the 5% probability level in a pairwise Tukey test). The growth of plot 3 over the 1995-1999 period is not presented, because a subsequent thinning occurred in this plot during this period. (**Figure adapted from Guillemot et al. (2015a)**).

Additionally, Fig. 3 shows that forest management, though thinning, has the potential to promote post-drought recovery of tree growth, as also reported in the study of Kohler et al., (2010); Misson et al., (2003) and Sohn et al., (2013). Moreover, because the inter-tree competition has been reported to promote drought-induced mortality (Linares et al., 2010; Ruiz-Benito et al., 2013), forest management may be an important tool for the mitigation of forest dieback induced by climate change (Allen et al., 2010). Another important aspect of forest management is the choice of the species composition and the degree of mixing (Paquette and Messier, 2011). A recent study revealed that species mixing promotes stand growth, especially on less productive sites (Toïgo et al., 2015). Overall, forest management and silviculture have the potential to promote forest productivity and/or mitigate forest vulnerability under climate change.

4. Simulating C allocation and forest management in process-

based models

Process-based models (also referred to as terrestrial biosphere models in the following) provide a framework to formalize biophysical hypotheses and combine knowledge about the physiological mechanisms that determine forest functioning and growth. PBMs can be evaluated at different temporal and spatial scales according to the process of interest (leaf or canopy matter and energy fluxes, stand or tree growth, or distributional range) and can therefore be used to investigate how tree functions will change in a changing environment (Cheaib et al., 2012; Keenan et al., 2011; Mäkelä et al., 2000; Medlyn et al., 2011).

However, PBMs strongly diverge in their predictions of the future forest productivity and important uncertainties remain about the evolution of the terrestrial C sink (Friedlingstein et al., 2006; Luo et al., 2014; Le Quéré et al., 2009). Among the different sources of uncertainty that currently flaw model projections, the within-tree C allocation may be of major importance. Carbon allocation has indeed long been considered as the Achilles' heel of PBMs (Rocha, 2013; Le Roux et al., 2001). Despite recent encouraging advances made on particular sites (Gea-Izquierdo et al., 2015; Li et al., 2014; Richardson et al., 2013; Schiestl-Aalto et al., 2015), the models used in regional and global C cycle projections do not perform well at predicting annual wood growth and wood stocks (Babst et al., 2013; De Kauwe et al., 2014). In a recent study, Friend et al., (2013) report that the simulated C residence time, which is partly determined by C allocation among tree organs, is a major source of uncertainty in process-based projections of the terrestrial C sink. Moreover, recent studies stressed the risk of getting the right answers for the wrong reason (Fatichi et al., 2014) when using the current generation of PBMs for predicting forest wood growth. Most of the models that are currently used to project future global C cycle indeed partition C into different tree compartments using empirical coefficients (Arora et al., 2013; Jones et al., 2013). These coefficients are typically fixed or they vary on a daily basis according to organ-specific phenology or functional equilibriums (Delpierre et al., 2015; Franklin et al., 2012; De Kauwe et al., 2014). In any case, the simulated wood growth is a fraction of the C entering the ecosystem during a given period (i.e., growth is limited by the source of C). This modelling approach has been challenged by the empirical evidences evocated above, and the implications of the sink limitations for the future of forest growth and wood stocks under climate change are yet to be quantified.

Besides, most PBMs simulate the functioning of an average tree rather than the functioning of

the whole forest. As a consequence, they cannot realistically simulate the impact of management on forest productivity or the effect on the age structure on the regional forest C balance of anthropized areas (Zaehle et al., 2006). In the context of global changes, the management of forest will have to rapidly adapt to the new environment experienced by the trees. PBMs simulating the stand structure and the impact of management on productivity can be an efficient decision tool to define the future silvicultural guidelines (Fontes et al., 2010; Mäkelä et al., 2000; Pretzsch et al., 2008). Moreover, the PBMs that do not represent explicitly the distribution of tree size features in the stand cannot be directly evaluated using an abundant data source in forest science: measurements from forest inventories, such as tree density or basal area (Bellassen et al., 2011a).

This introduction emphasises the need for a better understanding and a better representation in PBMs of the processes that underlie the productivity of forests over large environmental gradients.

5. Research objectives

Our main objective in this thesis was to move forward into our understanding of the constraints that affect - or will affect - the wood productivity in European forests, from the present period to the end of the 21st century. We addressed this objective through the improvement of the representation of the forest productivity and C allocation in a process-based model, building on a detailed analysis of the drivers of annual wood productivity in French forests over the last 30 years.

Our specific objectives were to:

- characterize the annual C allocation to wood along large environmental gradients over France
- to develop a new C allocation scheme in the CASTANEA model (Dufrêne et al., 2005) on the basis of our finding and results from the literature
- project the future of the wood productivity in European forests over the 21st century
- couple the CASTANEA model with an empirical stand structure module to evaluate the impact of management on wood productivity over France

6. Studied species

The study was conducted in five species that are widely distributed over Europe (Fig. 4), and representative of the main European forest biomes: *Fagus sylvatica*, *Quercus petraea* and *Quercus robur* for temperate deciduous broadleaf forests; *Picea abies*, for high-latitude and high-altitude evergreen needleleaf forests; and *Quercus ilex*, an evergreen broadleaf species from Mediterranean forests (Tutin, 1980). Because *Quercus petraea* and *Quercus robur* are difficult to distinguish in the field and have a high hybridization rate (Abadie et al., 2012), these two species were grouped in the analyses and are hereafter collectively referred to as temperate oaks.

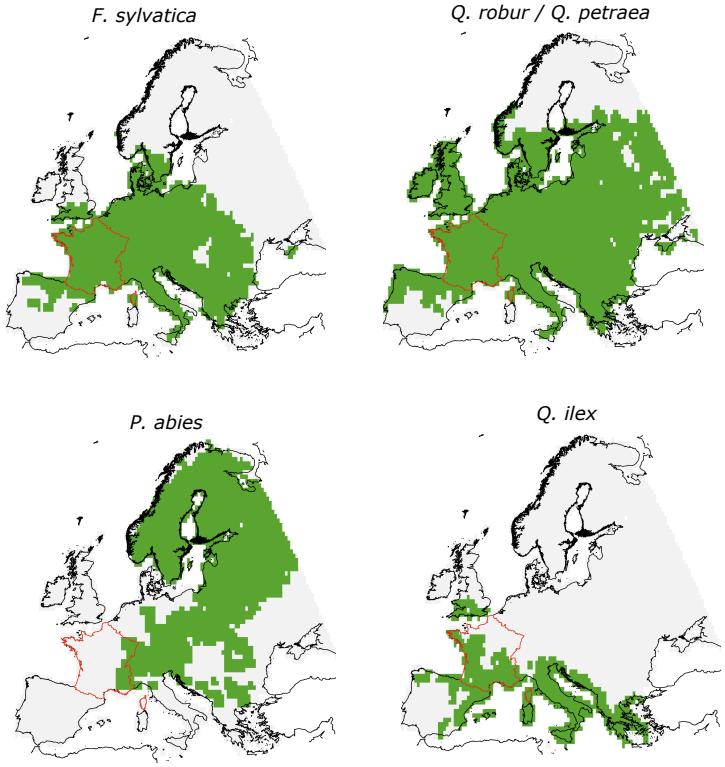

Figure 4: Spatial distribution of the studied species over Europe (0.5° resolution). Source: Atlas Florae Europaeae (http://www.luomus.fi/en/atlas-florae-europaeae-afe-distribution-vascular-plants-europe).

7. Overview of the CASTANEA model

The CASTANEA model (Dufrêne et al., 2005) is a stand growth model that simulates the water and carbon budget of even-aged, monospecific stands over a forest rotation. The model simulates the functioning of one average tree, i.e. the competition is not represented. CASTANEA explicitly considers a variety of physiological processes that are believed to influence forest functioning on the hourly to annual time scales (Fig. 5). In the following, we briefly

described the main features of the model. A complete description of CASTANEA can be found in Dufrêne et al., (2005), with subsequent modifications in Davi et al., (2009) and Delpierre et al., (2012).

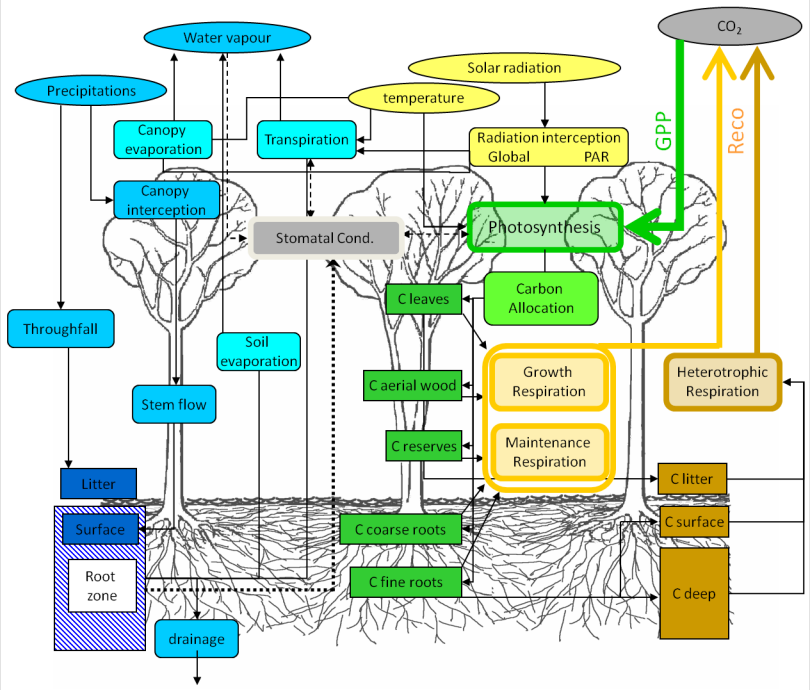

Figure 5: Flow diagram of the CASTANEA model. Right angle boxes are state variables (C and H_2O), rounded angle boxes are flow variables (C and H_2O) and elliptic boxes are forcing meteorological variables. Each arrow corresponds to a water or carbon flow from one compartment to the next one. Dotted arrows correspond to (1) the influence of soil water content on stomatal opening and (2) the stomatal control of both transpiration and photosynthesis. (**Figure adapted from Dufrêne et al. (2005)**).

- The C assimilation, autotrophic and heterotrophic respirations, and evapotranspiration are simulated on a half-hourly basis. The C assimilation is simulated using the biochemical approach suggested by Farquhar et al. (1980). The stomatal conductance is calculated using the model of Ball et al. (BWB model, 1987), and the coupling with assimilation follows the analytical solution of Baldocchi (1994). In case of water stress, the slope of the BWB model decreases linearly with the soil water content. We assume that water stress occurs when the soil water content drops below 40% of soil water holding capacity (Granier et al., 1999). Autotrophic respiration is divided between maintenance and growth respiration: maintenance respiration is function of temperature, using a typical Q10 relationship; growth respiration is function of organ growth rate and biochemical composition (De Vries, 1975). Heterotrophic respiration is simulated using a modified version of the CENTURY model (Le Dantec, 2000; Parton et al., 1987).

- The simulated canopy is assumed to be horizontally homogeneous and is vertically subdivided into a given number of layers, each of them enclosing a constant amount of leaf area (typically 0.1m^2leaf/m^2soil). The variation of the leaf physiological characteristics inside the canopy are simulated through the exponential decline of the leaf mass per area, while the nitrogen content per mass unit is fixed at a constant value (Ellsworth and Reich, 1993; Montpied et al., 2009). Radiative balance is simulated using the SAIL model (Verhoef, 1984). The stomatal conductance is calculated for each canopy layer and summed for the entire canopy. Canopy conductance then modulates the water gas exchange between the canopy and the atmosphere according to the Penman-Monteith equation (Monteith, 1965).

- The water budget is calculated on a daily basis. The soil water balance is simulated using a bucket model with three layers (litter, a top-soil layer and a total-soil root zone including top-soil layer). For each layer, water content is calculated daily as the difference between inputs (stem flow, throughfall and drainage from above layers) and outputs (evaporation, transpiration and drainage).

- The phenology of organs and the C allocation are simulated on a daily basis. The simulated stand comprised four functional compartments: foliage, woody biomass (that included stem, branches and coarse roots), fine roots and the pool of TNC, i.e., the reserve C pool. The onset and cessation of wood growth are fixed to constant days of the year, and the phenology of leaf is simulated using temperature sums (Delpierre et al., 2009a; Dufrêne et al., 2005). The allocation to reserve and fine roots can occur throughout the year but is strongly constrained by the C allocation to leaf and wood compartments. The C allocation is simulated as a fraction of the net primary production (NPP, i.e., the net balance between C assimilation and autotrophic respiration), using seasonally fixed proportion values (allocation coefficients, Dufrêne et al., 2005) that are determined to satisfy functional equilibria (Davi et al., 2009).

8. Description of the data sources

For this study, we mostly relied on the field measurements provided by two complementary sources.

- The RENECOFOR permanent plot network (Ulrich, 1997) that is managed by the Office

National des Forêts and comprises 101 sites over France, and the Puéchabon site (Rambal et al., 2014). The RENECOFOR and Puéchabon datasets comprises several extensive circumference surveys, a dendrochronological sampling and a number of ecological variables at each site (e.g., soil characteristics, leaf nitrogen content, litter collection, leaf phenology). The soil water holding capacity, leaf area index (LAI) and leaf nitrogen content that were derived from these measurement were used to force the model, reducing the uncertainty of the simulations. In addition, the biometric and dendrochronological measurements allowed the calculation of the past annual stand wood growth at each site. The RENECOFOR and Puéchabon datasets were therefore used (1) to assess the inter-site and inter-annual dependences of the C allocation to wood (**Chapter 2**), and (2) to evaluate the ability of the calibrated CASTANEA model to predict the inter-annual fluctuation of wood growth (**Chapter 3**). We also used the forest inventories conducted on the RENECOFOR network to calibrate the stand structure module, and to evaluate the performances of the coupling between CASTANEA and the stand structure module using stand basal areas and mean tree circumferences (**Chapter 4**).

- The National Forest inventory (NFI, http://inventaire-forestier.ign.fr/spip/). The NFI sampling method is based on temporary plots distributed over a systematic random grid of 1 km x 1 km, thus ensuring an exhaustive representation of French environmental gradients (Charru et al., 2010; Vallet and Pérot, 2011). Biometric data are collected within concentric circles of 6, 9 and 15 m according to the size of the trees: all trees with a circumference greater than 23.5 cm are measured in the 6 m circle, all trees with a circumference greater than 70.5 cm are measured in the 9 m circle, and all trees with a circumference greater than 117.5 cm are measured in the 15 m circle. Biometric measurements include circumference at breast height, 5 years of radial increment and total height. A relative weight is given to each measured tree, for upscaling at the stand level. The dataset also includes a reduced number of ecological variables that can be used to force the model (i.e., the soil characteristics). We used the NFI dataset to calibrate and evaluate the wood growth submodel of the C allocation scheme implemented in CASTANEA, using 5-year stand wood growth observations (**Chapter 3**).

Although, our focus was mainly on above-ground wood productivity, we also relied on two additional data sources related to C allocation in trees.

- The satellite-derived MODIS/TERRA daily surface reflectance product at a 250 m resolution (MOD09GQK, Earth Observing System Data Gateway) over the 2001-2012 period were extracted at each IFN plot and the normalized difference vegetation index (NDVI) were inferred. NDVI was used to calculate the LAI dynamic at each site (Myneni et al., 1995; Wang et al., 2005). We used the satellite-derived LAI data to calibrate the LAI submodel of the C allocation scheme implemented in CASTANEA (**Chapter 3**).

- Measurements of total non-structural carbohydrate (C reserve pool) were obtained from a global meta-analysis (A. Sala & J. Martínez-Vilalta, unpublished data) that comprise measurements of stem saplings and mature forest tree sapwood from throughout Europe. We used this dataset to provide species-specific benchmarks for the reserve pool predicted by CASTANEA (**Chapter 3**).

9. Organization of the dissertation

This dissertation consists of five chapters. Chapters 2 to 4 are included as stand-alone manuscripts that are either already published or in preparation.

In **chapter 2**, we provide an evaluation of the spatio-temporal dynamics of the annual C allocation to wood in French forests. Our study supports the premise that the growth of European tree species is subject to complex control processes that include both source and sink limitations. The relative influences of the growth drivers strongly vary with time and across spatial ecological gradients. We suggest a straightforward modelling framework with which to implement these combined forest growth limitations into PBMs.

This chapter has been published under the following reference: Guillemot, J., Martin-StPaul, N. K., Dufrêne, E., François, C., Soudani, K., Ourcival, J. M. and Delpierre, N.: *The dynamic of annual carbon allocation to wood in European forests is consistent with a combined source-sink limitation of growth: implications for modelling*, Biogeosciences Discussion, 12(3), 2213 2255, 2015 (Accepted in Biogeosciences).

We used the modelling framework designed in chapter 2 in the context of **chapter 3**, where we present a new C allocation scheme implemented in the CASTANEA model. The allocation

of C is represented using four compartments competing for C supply on a daily basis and integrates a combined source-sink limitation of wood growth. The new version of CASTANEA was calibrated and evaluated at stand scale over large environmental gradients over France. The calibrated model was then used to evaluate how the environmental limitations of the sink activity impacted the simulated changes in European forest growth over the 21st century.

This chapter appears as a draft, in preparation for Global Change Biology: Guillemot, J., Martin-StPaul, N. K., Dufrêne, E., François, Stéfanon, M., Hmimina, G., C., Soudani, K., Ourcival, J. M., Marie, G., Leadley, P. and Delpierre, N.: *Environmental control of the sink activity affects the projections of wood growth in European forests.*

In **chapter 4**, we address the issue of the representation of management effect on productivity in PBMs. The CASTANEA model was coupled to a stand structure module (SSM) based on empirical tree-to tree competition rules. The calibration of the SSM was based on a thorough analysis of inter-site and inter-annual variability of competition asymmetry. The coupled CASTANEA-SSM model was evaluated across France and used to compare the effect of contrasted silvicultural practices on simulated stand carbon fluxes and growth.

This chapter has been published under the following reference: Guillemot, J., Delpierre, N., Vallet, P., François, C., Martin-StPaul, N. K., Soudani, K., Nicolas, M., Badeau, V. and Dufrêne, E.: *Assessing the effects of management on forest growth across France: insights from a new functional structural model*, Annals of Botany, 114(4), 779 793, 2014.

Finally, the **chapter 5** provides brief general discussion and perspectives.

The appendices provide three additional studies on related topics that I authored or co-authored.

Appendix A1. Guillemot, J., Klein, E. K., Davi, H. and Courbet, F.: *The effects of thinning intensity and tree size on the growth response to annual climate in Cedrus atlantica: a linear mixed modeling approach*, Ann. For. Sci., 1 13, 2015.

Appendix A2. Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser,

T. and Rathgeber, C. B. K.: *Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models*, Ann. For. Sci., 10.1007/s13595-015-0477-6, 2015.

Appendix A3. Ay, J.S.$^{\Delta}$, Guillemot, J.$^{\Delta}$, Martin-StPaul, N.K.$^{\Delta}$, Doyen, L., Leadley, P.: *Accounting for land-use selection bias in tree species distribution models and revealing a hidden part of the niche.* Δ Equal contributions. (*In preparation*).

Chapter 2

The dynamic of annual carbon allocation to wood in European forests is consistent with a combined source-sink limitation of growth

1 Introduction

Forests play a critical role in the global carbon (C) cycle. Inventory-based estimates indicate that established forests have been a persistent carbon sink for decades, sequestering almost 30% of the world's total anthropogenic C emissions between 1990 and 2007 (Pan et al., 2011). The fate of the sequestered C is highly dependent on the C dynamic in trees, which determines the residence time of C in forest ecosystems. Despite its importance for the future terrestrial C sink (Carvalhais et al., 2014; Friend et al., 2013), the partitioning of C among tree organs and ecosystem respiration remains poorly understood (Brüggemann et al., 2011). In particular, there has been considerable amount of debate regarding the physiological mechanisms that drive the increment of the forest woody biomass (Palacio et al., 2014; Wiley and Helliker, 2012). The fraction of assimilated C stored in woody biomass can be inferred by combining biometric measurements with estimates of the C exchange between the ecosystem and atmosphere, based on the eddy-covariance (EC) technique (Babst et al., 2014; Litton et al., 2007; Wolf et al., 2011b). Global meta-analyses (that included data from various biomes and species) have revealed a strong correlation between the observed gross primary production (GPP) and the woody biomass increment (Litton et al., 2007; Zha et al., 2013). Accordingly, growth has long been thought to be C limited, because of the hypothesized causal link between C supply and growth (i.e., source control, Sala et al. 2012). The environmental factors that have been reported to affect growth (soil water content, temperature, nutrient content, light and CO_2) were therefore supposed to operate through their effects on photosynthesis and respiration fluxes. This C-centric paradigm underlies most of the C allocation rules formalized in the terrestrial biosphere models (TBMs) that are currently used to evaluate the effects of global changes on forests (Clark et al., 2011; Dufrêne et al., 2005; De Kauwe et al., 2014; Krinner et al., 2005; Sitch et al., 2003).

Source control of wood growth is a mechanism that has been questioned by several authors, who argue that cambial activity is more sensitive than C assimilation to several environmental stressors (Fatichi et al., 2014). In particular, the decrease in cell turgor that occurs because of water stress strongly affects cell division and expansion (Woodruff and Meinzer, 2011) before there is any strong reduction in the gas exchange (Muller et al., 2011; Tardieu et al., 2011). Similarly, cell division is more sensitive to a decrease in temperature than photosynthesis is, and stops at much higher temperatures (e.g. with a commonly cited limit threshold of +6°C)

than photosynthesis does (Körner, 2008). The onset of cambial activity is also known to be highly responsive to temperature (Delpierre et al., 2015; Kudo et al., 2014; Lempereur et al., 2015; Rossi et al., 2011) and, in turn, may partly determine annual cell production and wood growth (Lupi et al., 2010; Rossi et al., 2013). Finally, the quality and quantity of available soil nutrients, particularly nitrogen (N), could affect growth independently of their impacts on C assimilation, because of the relatively constrained stoichiometry of tree biomass (Leuzinger and Hättenschwiler, 2013). These studies suggest that growth is limited by the direct effects of environmental factors (i.e., sink control). However, numerous key environmental factors (e.g., nutrients, temperature and water) affect both sink and source activities, and it is thus difficult to determine whether wood growth is more related to C supply or to the intrinsic environmental sensitivity of cambium functioning (Fatichi et al., 2014). The extent to which wood growth is under source or sink control is of paramount importance for predicting how trees will respond to global changes and specifically how increasing atmospheric CO_2 will affect forest productivity and the future terrestrial C sink. The implementation of the respective roles of source and sink controls on growth in TBMs is therefore a substantial challenge for modellers, because it may determine our ability to project future forest C sink, diebacks and distributions (Cheaib et al., 2012; Fatichi et al., 2014; Leuzinger et al., 2013).

The allocation of assimilated C within forest ecosystems is a complex, integrative process that can be described by several non-exclusive principles (Franklin et al., 2012) that include i) allometric scaling, ii) functional balance and iii) evolution-based optimal responses. i) The allometric scaling principle is based on the assumption that biophysical laws, such as the mechanical constraints associated with plant hydraulic architecture and the construction of water-transport system (Magnani et al., 2000), determine C partitioning among the different tree compartments. ii) The functional balance principle suggests that the organ responsible for acquiring the limiting resource is preferentially allocated C. Consistent with this principle, higher C allocation to fine roots at the expense of C allocation to wood growth has been reported for poor or dry soils (Chen et al., 2013; Keyes and Grier, 1981). In addition, a possibly greater allocation to root symbionts and exudates at the expense of biomass production has also been reported (Vicca et al., 2012). iii) Finally, the optimal response principle postulates that allocation maximizes fitness in a fixed environment. This hypothesis agrees with the idea that a dynamic reserve pool act as temporary storage, possibly at the expense of growth, to promote long-term

tree survival (Chapin et al., 1990; Sala et al., 2012). Indeed, time lags between C uptake and growth have been reported (Gough et al., 2009; Richardson et al., 2013). The optimal response principle is consistent with several well-known life history traits, such as preferential allocation to reproduction in ageing plants, which could lead to age-related declines in woody biomass allocation (Genet et al., 2010; Thomas, 2011). The woody biomass increment therefore appears to be under the control of multiple factors. The effects of these drivers are expected to strongly vary in space and time. Consequently, studies have reported conflicting relationships between the C supply and wood growth (Gielen et al., 2013; Richardson et al., 2013), ranging from no significant relationships (Mund et al., 2010; Rocha et al., 2006) to close relationships on seasonal (Babst et al., 2014; Granier et al., 2008; Zweifel et al., 2010) or annual (Ohtsuka et al., 2009; Peichl et al., 2010; Zweifel et al., 2010) time scales. Determining the key processes that affect wood growth on different spatio-temporal scales is necessary to explain these apparently contradictory results using a common framework. Moreover, investigations should be conducted at the species level, because phylogeny may strongly constrain forest functioning (Carnicer et al., 2013; Drobyshev et al., 2013) and induce different growth determinants among taxa (Genet et al., 2010).

There is a gap between the knowledge obtained from global studies of universal C allocation rules in forests and our understanding of the cell processes that underlie cambial activity; currently, this gap appears to be the primary obstacle to a more complete understanding of wood growth drivers. In this regard, species-specific studies that evaluate the dynamic of C partitioning to annual wood growth along soil and climate gradients would be highly useful but are lacking. Unfortunately, there is a scarcity of datasets that combine EC and growth measurements at the same sites (Luyssaert et al., 2007). Here, we circumvented this limitation by complementing stand and soil measurements at a French permanent plot network of 49 forest sites with process-based simulations of annual and seasonal tree C balance (Fig. 1). Simulations were performed using a process-based model (CASTANEA, Dufrêne et al. 2005) that was thoroughly validated using EC data from throughout Europe (Davi et al., 2005; Delpierre et al., 2009b, 2012) and was applied using site-specific parameters. By relating biometric measurements to variables that explain the C source and sink activity, we evaluated the key drivers of the annual C allocation to stand wood growth in five species that are representative of the main European forest biomes: *Fagus sylvatica*, *Quercus petraea* and *Quercus robur* for temperate

deciduous broadleaf forests; *Picea abies*, for high-latitude and high-altitude evergreen needleleaf forests; and *Quercus ilex*, an evergreen broadleaf species from Mediterranean forests. Specifically, the relative influence of annual and seasonal (from one month to the year) tree C balance (source control), direct environmental control (water and temperature effects on sink activity) and allocation adjustments related to age, past climate conditions, competition intensity and soil nutrient availability on tree growth were considered (Fig. 1). We aimed to (1) quantify the relative contributions of source and sink controls to the spatio-temporal dynamic of forest wood growth across a wide range of environmental contexts and (2) provide information that can be used to refine the representation of forest growth causalities in TBMs.

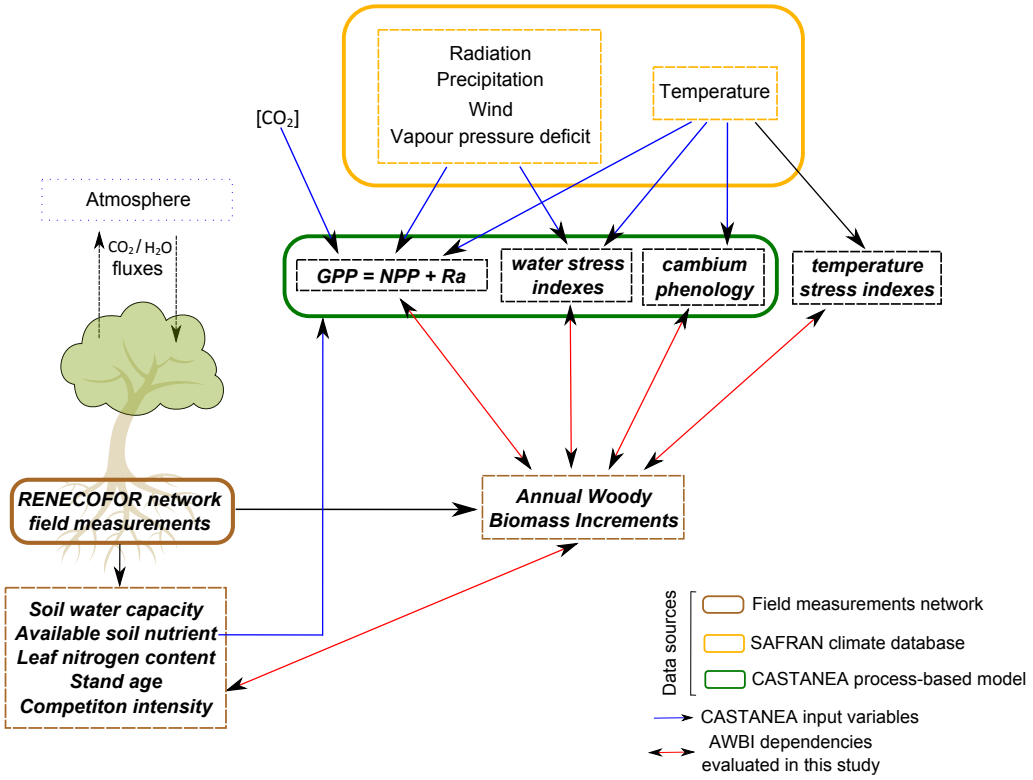

Figure 1: The conceptual framework and the three sources of data (field measurements, climate reanalysis, and process-based simulations) used in the analyses.

2 Materials and methods

We based our analyses on three complementary data sources: field measurements, climatic variables from atmospheric reanalysis (Vidal et al., 2010) and process-based simulation data. This hybrid approach allowed us to assess and disentangle the effects of previously reported environmental and endogenous drivers of C allocation to wood growth (Fig. 1).

2.1 Study sites and field data

We gathered field measurements from 48 plots from the French Permanent Plot Network for the Monitoring of Forest Ecosystems (RENECOFOR, Ulrich, 1997) and the Puéchabon tower flux site (Martin-StPaul et al. 2013). The location and general climatic features of these plots are shown in Fig. 2 and Table 1. Complete site description is available in Supplement S1.

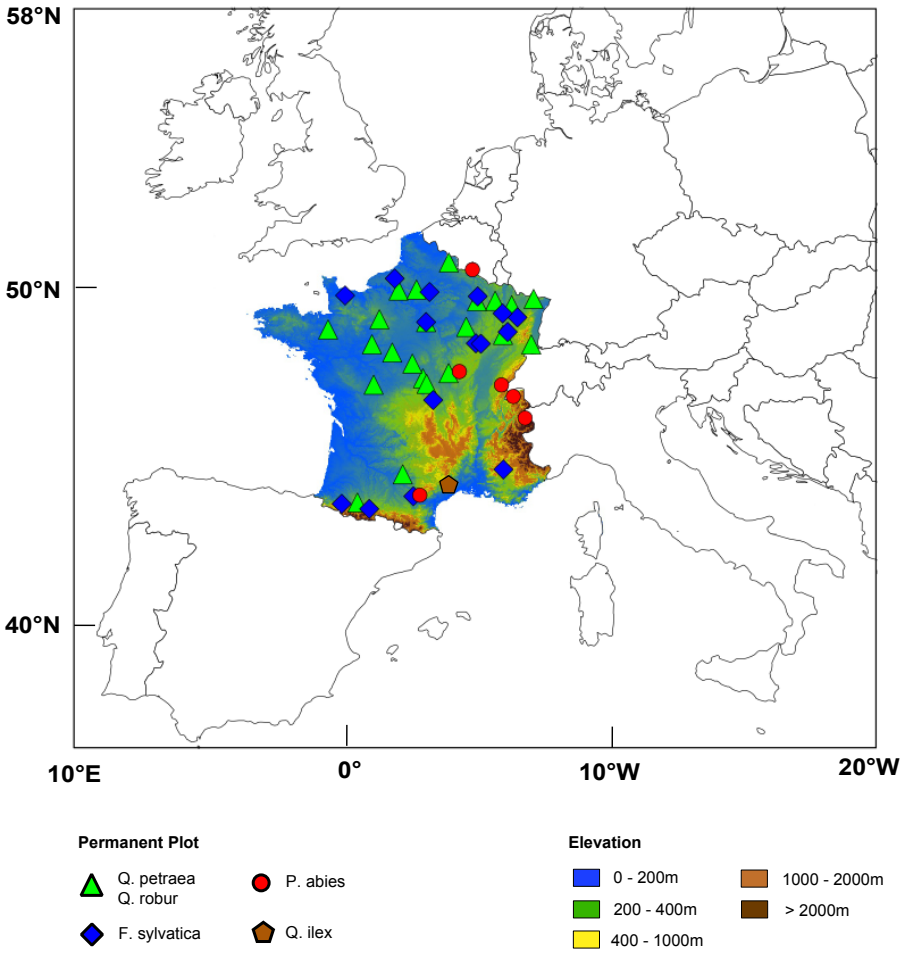

Figure 2: Locations of the study sites.

Species	Number of plots	Number of site-years	Elevation (m)	ETP (mm)	Precip. (mm)	Temp. (°C)	Source
F. sylvatica	16	313	565 ± 326	1010 ± 121	1001 ± 133	10.1 ± 0.98	RENECOFOR
Q. petraea/Q. robur	26	484	193 ± 76	999 ± 71	821 ± 96	10.7 ± 0.63	RENECOFOR
P. abies	6	101	1056 ± 313	933 ± 44	1559 ± 340	7.1 ± 1.4	RENECOFOR
Q. ilex	1	43	270	1417	907	13.4	Puéchabon site

Table 1: Climate of the study sites. ETP: annual Penman - Monteith potential evapotranspiration; Precip.: annual precipitation; Temp.: annual temperature. Values are site averages ± standard deviation among sites.

2.1.1 Growth measurements and historical stand growth reconstruction

Growth measurements were obtained by two methods: i) *Dendrochronological sampling*, in which 12 to 30 overstory trees per plot were cored to the pith at breast height with an incremental borer. Cores were collected in 1994 at the RENECOFOR sites and in 2008 at the Puéchabon site (Lebourgeois 1997; J.M. Ourcival, *unpublished data*). Tree circumferences at breast height (CBHs) and total heights were also measured. The average stand age was inferred from the tree ring series. ii) *Forest inventories*, in which extensive CBH surveys were conducted in a 0.5 ha area of every plot (Cluzeau et al. 1998; Gaucherel, Guiot & Misson 2008; J.M. Ourcival, unpublished data).

Tree ring series were combined with the CBH surveys to reconstruct the historical CBHs of every tree on the plots (over 8 to 43 years, Supplement S1). The entire stand tree CBH distribution was reconstructed from the CBHs of the sampled trees using an empirical tree competition model (Deleuze et al., 2004). This model stipulates that only trees with a CBH above a given threshold (σ, the minimum circumference needed to gain direct access to sunlight), have a significant growth. Overstory trees then have an annual basal area growth rate that is proportional to their size, according to a slope coefficient, γ. Following the work of Guillemot et al. (2014, Chap. 4), the model was calibrated annually, beginning at year (n) of the core sampling and used iteratively to reconstruct the past stand CBH growth. The σ parameter was first defined using an empirical relationship with the maximum CBH of the stand tree distribution from year (n). The γ parameter was then adjusted using the tree rings measured on the sampled trees in year (n-1). The parameterized model was finally used to predict the basal area increments of all the trees in the distribution, and consequently the tree CBH distribution in the year (n-1). A detailed description of the iterative process can be found in Supplement S2 and in Guillemot et al. (2014, Chap. 4).

The inferred past trajectory of the stand CBH distribution was used to calculate the historical number of stems (*numstem*, Table 2) and stand basal area, which we considered to be a proxy for within-stand competition intensity (*SBA*, Table 2, Kunstler et al. 2011). The historical total woody stand biomass was also calculated (Supplement S3) using species-specific tree level allometric functions (Bontemps et al., 2009, 2012; Dhôte and Hercé, 1994; Seynave et al., 2005; Vallet et al., 2006) and wood density models (Bouriaud et al., 2004; Wilhelmsson et al., 2002;

Zhang et al., 1993). For *Q. ilex*, we used the appropriate function from Rambal et al. (2004) to calculate the stand woody biomass from CBHs. Past annual woody biomass increments (AWBIs) were then inferred (Supplement S4).

IDs	Description	Unit	Type	Scale
age	Stand age	years	M	S
AWBI	Annual woody biomass increment	$g C m^{-2}$	M	ST
SBA	Stand basal area	m^2	M	S
camb_onset	Onset of the cambial activity	day of the year	S	T
GPP_{gp}	Gross primary production of the current (y) growth period	$g C m^{-2}$	S	ST
GPP_{y-1}	Gross primary production of the previous ($y-1$) year	$g C m^{-2}$	S	T
frost	Sum of the average daily temperatures below $-2\,^{\circ}C$ during the last winter (year y-1 and y)	$^{\circ}C$	C	ST
LNC	Leaf nitrogen content	$g N g DM^{-1}$	M	S
NPP_{gp}	Net primary production of the current (y) growth period	$g C m^{-2}$	S	ST
NPP_{y-1}	Net primary production of the previous ($y-1$) year	$g C m^{-2}$	S	T
numstem	Stem density	$number\,ha^{-1}$	M	S
SNA	Class of soil nutrient availability (1: low, 2: medium, 3: high)	unitless	M	S
SWC	Soil water holding capacity	mm	M	S
templim	Number of days of the current (y) growth period with an average temperature below $6\,^{\circ}C$	number of days	C	ST
Ra_{gp}	Autotrophic respiration of the current (y) growth period	$g C m^{-2}$	S	ST
Ra_{y-1}	Autotrophic respiration of the previous ($y-1$) year	$g C m^{-2}$	S	T
WS_per_{gp}	Number of days of the current (y) growth period with a soil water content below 60 % of the soil water holding capacity	number of days	S	ST
WS_per_{y-1}	Number of days of the previous ($y-1$) year with a soil water content below 60 % of the soil water holding capacity	number of days	S	T
WS_int_{gp}	Water stress intensity index over the current (y) growth period	unitless	S	ST
WS_int_{y-1}	Water stress intensity index of the previous ($y-1$) year	unitless	S	T

Table 2: The Type category indicates the source of the data: field measurement (M), SAFRAN climate database (C) or CASTANEA simulation (S). The Scale categories indicate whether the variable was considered in the spatial (S) and temporal (T) analyses.

2.1.2 Measurements of stand characteristics

The stand measurements included the soil water holding capacity (SWHC), leaf area index (LAI), leaf N content (LNC) and soil nutrient availability (SNA). The SWHC was estimated via the soil depth and texture measured at two soil pits per plot (Brêthes and Ulrich, 1997). The LAI was estimated from litter collection (Pasquet, 2002), and the sunlit LNC was determined annually for 8 trees between 1993 and 1997 (Croisé et al., 1999).

SNA was assessed as the soil's C:N biomass ratio, the absolute value of the cation-exchange capacity and the per cent base saturation (Ponette, 1997). These soil indices were measured at 3 depths (0 to 10, 10 to 20, 20 to 40 cm) and were used to categorize the soil plots into three nutrient classes, from low to high nutrient availability (Supplement S5). The SNA, SWHC and

LNC were used to characterize plot fertility in the statistical analyses (Table 2).

2.2 Climate data

The following meteorological variables at the hourly temporal scale (with 8km spatial resolution) were obtained from the SAFRAN atmospheric reanalysis (Vidal et al., 2010): global radiation, rainfall, wind speed, air humidity and air temperature. Temperature, which was related to the average altitudes of the SAFRAN cells, was corrected using plot-specific elevation measurements (assuming a lapse rate of 0.6 °K per 100 m, Supplement S1). These variables were used for climate forcing in the CASTANEA model (Dufrêne et al. 2005, see the following section). In addition, two annual temperature indices were used as proxies of winter frost damage and low temperature stress during the growing period (frost and $\text{templim}_{\text{gp}}$, respectively, Table 2).

2.3 Process-based simulation data

We used the CASTANEA model to simulate an ensemble of diagnostic variables that are related to the C source and sink activity of forest stands: the elementary components of the tree C balance, bioclimatic water stress indices and the onset of the biomass growth. The eco-physiological process-based CASTANEA model aims to simulate C and water fluxes and stocks of a monospecific, same-aged forest stand on a rotation time scale. The hourly stand-atmosphere C fluxes predicted by the CASTANEA model have been thoroughly validated using EC data from throughout Europe (Davi et al., 2005; Delpierre et al., 2009b, 2012). Importantly, the biophysical hypotheses that were formalized in this model are able to reproduce the interplay of the complex mechanisms that lead to inter-annual variability in the stand C balance (Delpierre et al., 2012); modelling this interplay has been recognized as a substantial challenge for TBMs (Keenan et al., 2012a). A complete description of CASTANEA is provided in Dufrêne et al. (2005), and subsequent modifications are described in Davi et al. (2009) and Delpierre et al. (2012). For the purpose of the present study, CASTANEA was parameterized with site-specific SWHC and LNC values. The measured LAI and total woody biomass were used to initialize the model simulations. The model's ability to reproduce the annual variability in LAI and the forest growth has been recently validated (Guillemot et al., 2014, Chap. 4). Nevertheless, the annual standing woody biomass was forced to conform to the observed values, because the model was

used for diagnostic purposes in this study.

Several groups of variables were simulated and aggregated on an annual basis (Table 2):

- *The elementary components of the tree C balance.* These components included the GPP, autotrophic respiration (Ra), and net balance (i.e., net primary productivity, NPP = GPP Ra). For a given year y, we aggregated the hourly simulated C fluxes over different seasonal time periods, with starting days that ranged from 30 to 190 and ending days that ranged from 190 to 350, at a 2-day resolution. The C fluxes were also summed i) for the species-specific biomass growth periods reported in the literature (GPP_{gp}, Ra_{gp} and NPP_{gp}, Supplement S6) and ii) for the entire preceding year (y-1) as a proxy of the forest C status induced by past climate conditions (lagged effect, GPP_{y-1}, Ra_{y-1} and NPP_{y-1}).

- *Bioclimatic water stress indices.* These indices included the intensity and duration of water stress (WS_int_{gp} and WS_per_{gp}, respectively, Supplement S7) during species-specific growing periods that have been reported in the literature (Supplement S6). The CASTANEA model simulated the daily soil water balance, based on a bucket soil sub-model with 2 layers (a top soil layer and a total soil layer that includes the top soil layer, Dufrêne et al., (2005)). WS_int_{gp} was then used to quantify the intensity of water stress by summing the reduc index on a daily basis (Granier et al., 1999).

$$reduc_t = \max\left(0, \min\left(1, \frac{SWC_t - SWC_{wilt}}{0.4 \times \left(SWC_{fc} - SWC_{wilt}\right)}\right)\right) \quad (1)$$

where SWC_t is the soil water content on day t (mm), SWC_{wilt} is the soil water content at the wilting point (mm) and SWC_{fc} is the soil water content at field capacity (mm). WS_per_{gp} is the number of days of the current growth period during which the soil water content was less than 60% of the soil water holding capacity (Table 2, modified from Mund et al., (2010)). Water stress indices were also calculated for the entire preceding year (lagged effect of water stress, WS_int_{y-1} and WS_per_{y-1}).

- *The onset of the biomass growth* (camb _onset). We used a new growth-onset module

(David, (2011); N. Delpierre and N. K. Martin-StPaul, *unpublished results*) based on a temperature sum trigger (Supplement S8).

2.4 Statistical analyses

2.4.1 General overview

Statistical analyses were conducted in three complementary steps for each studied species. (1) We calculated the correlation of the AWBIs and the C fluxes (GPP, NPP and Ra) aggregated seasonally (from 1 month to one year) to evaluate the relationship between the C supply and annual biomass growth changes. (2) The dependences of the AWBIs on the C source and the sink activity were evaluated on an inter-site spatial scale to determine the influence of the site characteristics on biomass growth. The relationship between the age and C allocation to woody biomass was also evaluated in this step. By using the age differences among sites, our chronosequence included a large range of ages (including stands that ranged in age from approximately 30 to 150 years-old, Table S1). (3) Finally, the drivers of AWBI were assessed temporally to determine the factors that were responsible for variability in the inter-annual biomass growth.

Because many environmental factors affect both forest sink and source activities, there may be strong covariance among the tree C balance and proxies of environmental stress (Fatichi et al., 2014) that could hamper the inferential power of classical statistical tests (Graham, 2003). However, the explanatory variables used in this study generally had correlation coefficients of less than 0.7, the level above which collinearity begins to severely affect model performance (Dormann et al., 2013). One exception was the correlation of components of the tree C balance (because NPP = GPP - Ra). Consequently, the tree C balance components were introduced one at a time into the models. In addition, temporal growth dependencies were evaluated using the random forest (RF) learning method (Breiman, 2001). A number of studies have empirically demonstrated the effectiveness of RF at identifying the true predictors among a large number of correlated candidate predictors (e.g., Archer and Kimes, 2008; Cutler et al., 2007; Genuer et al., 2010). The explanatory variables considered in our spatial and temporal analyses are presented in Table 2 and Fig. 1. Analyses were conducted with the R software (R Development Core Team 2013), using the packages lme4 (Bates et al., 2007), randomForest (Liaw and Wiener, 2002) and

MuMIn (Barton and Barton, 2014). Because *Quercus petraea* and *Quercus robur* are difficult to distinguish in the field and have a high hybridization rate (Abadie et al., 2012), these two species were grouped in the analyses and are hereafter collectively referred to as temperate oaks.

2.4.2 Correlations between growth and C fluxes

Pearson correlations between the AWBIs and simulated C fluxes in different seasonal time periods were calculated separately for each site. The highest median correlation value for each species was retained and tested against zero using Wilcoxon signed rank tests. Critical correlations (i.e., the threshold values for a significant difference with the retained maximum correlation) were determined to evaluate the sensitivity of the correlation values to changes in the C flux aggregation periods.

2.4.3 Drivers of spatial variations in biomass growth

The drivers of spatial variations in biomass growth were evaluated using multiple regression models using an information-theoretic approach (Burnham and Anderson, 2002). The AWBIs and the considered explanatory variables were averaged for each plot. The variables introduced into the linear models were centred and scaled such that their normalized coefficient estimates indicated the relative influence of the predictors on the AWBI. The elementary components of tree C balance (NPP, GPP and Ra) were introduced one at a time into the models. For each species, multiple regression models that contained all possible combinations of the explanatory variables were fitted. The models were compared using the second-order Akaike information criterion (AIC), and all models with an Akaike weight of at least 1% of the best approximating (lowest AIC) model were considered to be plausible (Burnham and Anderson, 2002). Ultimately, we retained the variables that appeared in at least 95% of the selected models. Models fitted using *P. abies* data were restricted to a maximum of 3 explanatory variables because of the small sample size (n=6, Table 1). *Q. ilex* (n=1) was not considered in the spatial analyses. The uncertainty of the simulated C fluxes was assessed in the analyses using a bootstrap procedure (Chernick, 2011): all linear models were fitted 1000 times, and at each iteration, the C flux values were randomly sampled within the root mean square error of the CASTANEA simulations (Supplement S9) to obtain a parameter estimate distribution for each variable. We finally

retained the explanatory variables with parameter estimate distributions that excluded the zero value at a two-tailed probability level of 5%.

2.4.4 Drivers of temporal variations in biomass growth

A temporal analysis was conducted on the standardized AWBI series: a double-detrending process was applied to each series based on an initial linear regression model, followed by fitting a cubic smoothing spline with a 50% frequency response cut-off (Mérian et al., 2011). For analysing the temporal variations in biomass growth we used an RF learning method (Breiman, 2001), which was possible because of the large sample size (n = 931 site-years). The RF learning method is a non-parametric method that is used to rank the contribution of different explanatory variables and evaluate their marginal effects on a variable of interest without assuming an a priori dependence. The RF method combined 500 binary decision trees that were built using bootstrap samples from the initial dataset. The decisions trees aimed to reduce the heterogeneity of the explained variable in the resulting branches. For each of the 500 trees, the data that were not involved in the tree construction were used for validation. The tree predictions and errors were then averaged to provide the final RF results. The RF method does not overfit or require cross-validation (Cutler et al., 2007). A subset of explanatory variables was randomly chosen at each node, thus reducing the effect of collinear variables on the output. The RF method was used to select variables that explained the temporal variability in biomass growth (Genuer et al., 2010). Variable selection relied on permutation importance, i.e., the existence of an increase in the global mean square error when a given variable was randomized in the validation subsamples. The forms of the dependences were illustrated by partial dependence plots (graphical depiction of the marginal effect of a given variable, Cutler et al. 2007). We used this information (variable selection and dependence forms) to test for the significance of the temporal AWBI dependences within the linear model. The uncertainty in the simulated C fluxes was considered in the linear models, following the procedure described in the spatial analysis section.

3 Results

3.1 Relationship between woody biomass growth and C fluxes

The elementary components of the simulated seasonal tree C balance differed in terms of their relationships with the inter-annual variability of the annual woody biomass increments (AWBI, Table 3). The simulated seasonal GPP and NPP were linked to AWBIs with a comparable agreement between species. However, the simulated Ra had weak and often non-significant relationships with the AWBIs across the 49 studied plots. The strongest correlations were obtained for flux aggregation periods that i) were generally consistent within a species for GPP and NPP but different for Ra and ii) strongly differed among species (Table 3).

Species	GPP				Ra				NPP			
	start	end	*r*	σ	start	end	*r*	σ	start	end	*r*	σ
F. sylvatica	124	258	0.62^{**}	0.18	96	200	-0.29^{*}	0.33	126	262	0.58^{**}	0.24
Q. petraea/Q. robur	136	214	0.59^{**}	0.25	98	192	0.31^{*}	0.24	130	214	0.50^{**}	0.28
P. abies	32	262	0.52^{**}	0.38	78	348	0.11	0.52	32	200	0.49^{**}	0.29
Q. ilex	186	226	0.60		36	256	−0.26		186	226	0.58	

Table 3: Relationships of annual wood growth and the components of the seasonal forest carbon balance: NPP, GPP and Ra. The *start* and *end* terms (day of the year) indicate the carbon flux period that yielded the maximum value for the median of the growth-flux correlations among sites. The r term is the maximum obtained for the median of the site-specific Pearson correlation coefficients; values that are significantly different from 0 are indicated (* indicates $P < 0.05$ and ** indicates $P < 0.001$). The σ term is the standard deviation of the Pearson correlation values among sites.

The coefficients of variation of the simulated annual NPP, GPP and Ra across the 49 studied sites were 10.8% ± 3, 7.4% ± 2, and 6.8% ± 3, respectively. GPP and NPP were summed from the beginning of May to the beginning of August and September, in temperate oaks and *F. sylvatica*, respectively. The longest GPP and NPP aggregation periods were obtained for *P. abies* (from the beginning of February to mid-September), and the shortest period were found for *Q. ilex* (from the beginning of July to mid-August). Minor (less than 20 days) changes in the flux aggregation period associated with the maximum simulated flux-AWBI correlation usually marginally affected the correlation values (Supplement S10). Consequently, aggregation periods that were less than 13 days different (either in terms of their starting or ending dates) from the values reported in Table 3 were generally not significantly lower than the maximum values (see the critical values presented in Supplement S10).

3.2 Spatial dynamic of C allocation to woody biomass growth

The inter-site variability in biomass growth was well explained by the selected multiple regression models ($R^2 \geq 0.6$). We highlighted that species varied in terms of their inter-site dependences (Table 4).

Species	Estimates				
	GPP_{gp}	age	SBA	P	adj. R^2
Q. petraea/Q. robur		-8.88×10^{-1} [39.5]	4.27×10^{-1} [19.5]	$< 10^{-4}$	0.69
F. sylvatica	5.07×10^{-1} [59.4]	-6.96×10^{-1} [61.6]		$< 10^{-4}$	0.88
P. abies	8.25×10^{-1} [8.6]			0.04	0.60

Table 4: Spatial dependences of annual wood growth: multiple regression estimates. The data have been centred and scaled. GPP_{gp} is the GPP of the growth period, age is the average age of the stand, and SBA is the stand basal area (Table 2). Values: estimates [F values]. All estimated values differed significantly from 0 ($P < 0.001$). All variables were retained in the bootstrap procedure (see main text).

The simulated C supply during the growth period (GPP_{gp}, Table 2) was positively correlated with biomass growth in *F. sylvatica* and *P. abies*, whereas there was no significant relationship between the average AWBI and photosynthesis among sites for temperate oaks (Fig. 3A). Notably, the final models did not include NPP_{gp} or Ra_{gp} for any species. The stand age was an important driver of biomass growth in temperate oaks and *F. sylvatica*. The stand age explained a substantial portion of the AWBI:C supply ratio in all species, although the relationship was not significant for *P. abies* (Fig. 3B). The fraction of C sequestered in woody biomass decreased with stand age (Table 4, Fig. 3B) and was reduced by half in temperate oaks and *F. sylvatica* stands that were between 50 and 150 years of age (from 0.3 to 0.13 and from 0.25 to 0.1, respectively). Additionally, we identified a significant and positive effect of stand basal area on both AWBI (Table 4) and the AWBI:GPP_{gp} ratio (*data not shown*) in temperate oaks.

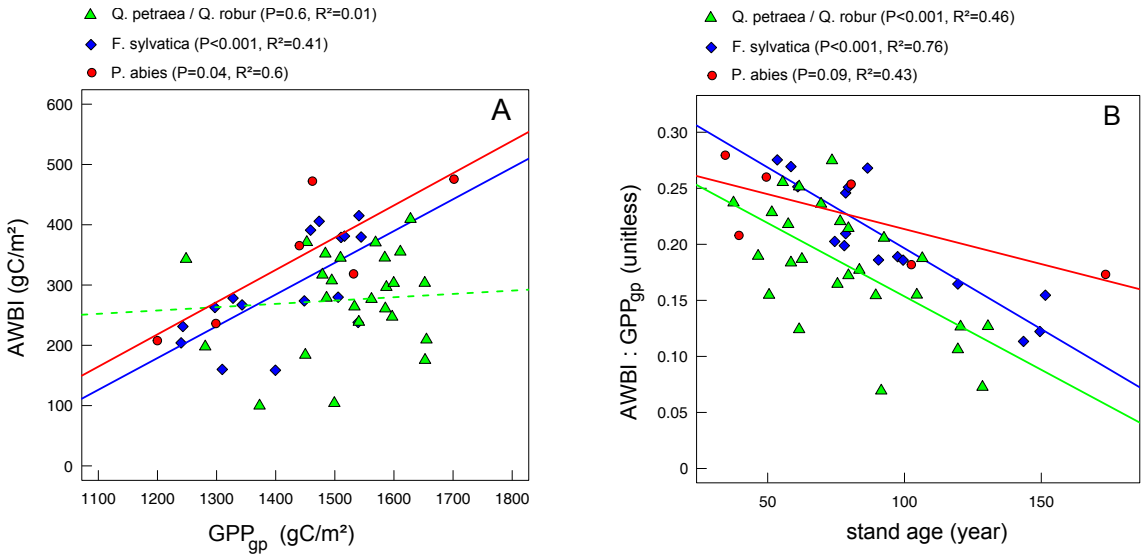

Figure 3: Spatial dependences of annual wood growth. A: Relationship of the AWBI and the GPP of the growth period (GPP_{gp}) averaged over sites. B: Age-related decline of the C partitioning to AWBI ($AWBI : GPP_{gp}$).

3.3 Temporal dynamic of carbon allocation to woody biomass growth

The ranking of the drivers of biomass growth obtained using the RF algorithm indicated that the temporal AWBI dependences varied among species (Fig. 4). The growth of temperate deciduous species was under a more complex environmental control than the growth of *P. abies* and *Q. ilex*, with several variables explaining a substantial portion of the annual variability in AWBI (Fig. 4A, B).

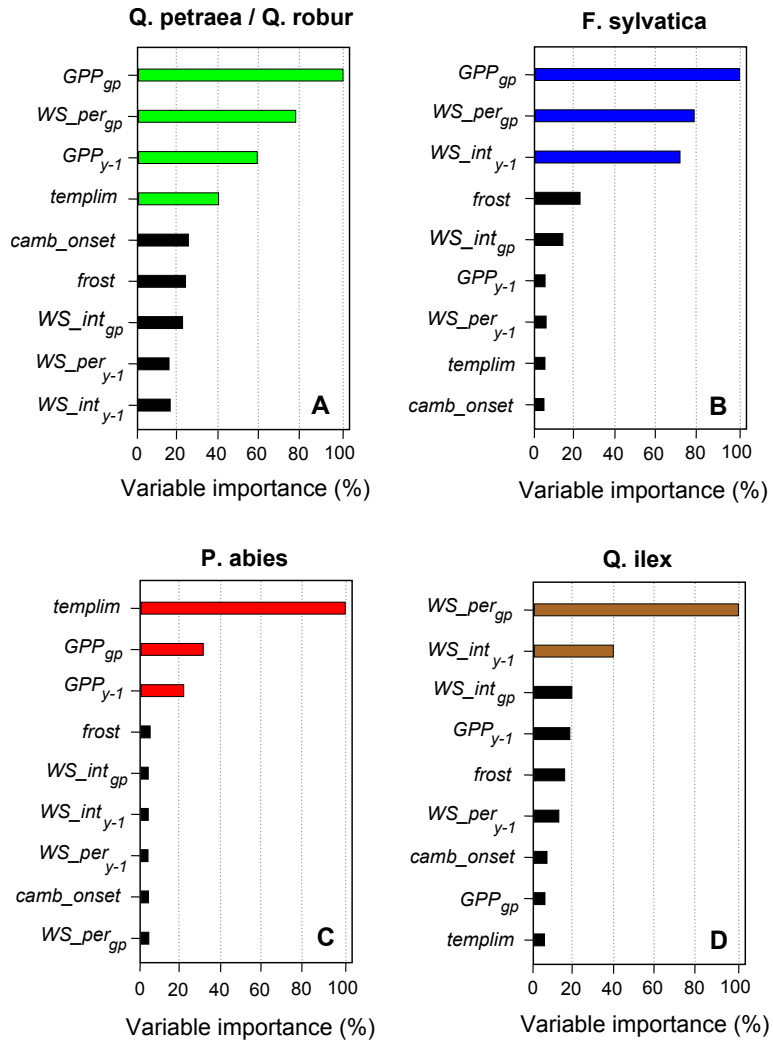

Figure 4: Temporal dependences of annual wood growth: the roles of explanatory variables from RF classification. Variable importance is expressed as the percentage of the importance of the top-ranked explanatory variable. The variable identifiers (IDs) are listed in Table 2. The coloured variables were retained in subsequent analyses.

Simulated C supply (GPP_{gp}) was strongly related to the AWBI of temperate oaks and *F. sylvatica* and, to a lesser extent, *P. abies* (Fig. 4A, B, C), with positive marginal effects (Fig. 5 a, e, h). The duration of water stress during the growth period (WS_per_{gp}) was the predominant driver of the AWBI variability of *Q. ilex*, and was also strongly related to growth in temperate deciduous species. Low temperatures during the growth period ($templim_{gp}$) most substantially affected *P. abies* and also explained a portion of the variability in AWBI of temperate oaks. The simulated water and temperature stress indices had negative and quasi-linear marginal effects on the AWBI (Fig 5). Finally, environmental lagged effects contributed substantially to the AWBI variability in all species: the water stress intensity of the previous year ($WS\_int_{y\text{-}1}$) affected the growth of *F. sylvatica* and *Q. ilex*, whereas the simulated C supply of the previous year ($GPP_{y\text{-}1}$)

affected temperate oaks and *P. abies*. Lagged effects generally revealed threshold in marginal dependences, with a significant negative effect on AWBI only under high water stress or low C supply (Fig. 5). The effects of the retained variables (Fig. 4) were evaluated via multiple regression models that used dummy variables to test for the significance of slope changes when thresholds appeared on partial plots (Fig. 5). The models explained approximately 20% of the variability in the AWBI for temperate oaks and *P. abies*, and approximately 40% of the variability for *F. sylvatica* and *Q. ilex* (Table 5).

Estimates	Species			
	Q. petraea/ *Q. robur*	*F. sylvatica*	*P. abies*	*Q. ilex*
GPP_{gp}	3.26×10^{-1} *** [96.7]	4.87×10^{-1} *** [133.7]	2.4×10^{-1} * [3.5]	
WS_per_{gp}	-1.09×10^{-1} ** [5.9]	-2.04×10^{-1} *** [13.5]		-5.8×10^{-1} *** [25.2]
WS_int_{y-1}		-2.37×10^{-1} *** [21.1]		-2.2×10^{-1} * [6.3]
GPP_{y-1}	3.82×10^{-1} * [3.3]		-4×10^{-1} ** [3.2]	
templim	-9.60×10^{-2} **$^{\Delta}$ [6.4]		-1.26^{***} [3.5]	
*D*1			-2.4×10^{-1} *** [0.4]	
*D*2	-3.9×10^{-1} ** [0.8]			
$D1 \cdot GPP_{gp}$			1.33^{**} [8.2]	
$D2 \cdot GPP_{y-1}$	-4×10^{-1} ** [6.4]			
ρ	0.61	0.68	0.52	0.44
P	$< 10^{-4}$	$< 10^{-4}$	7.7×10^{-3}	$< 10^{-4}$
adj. R^2	0.21	0.42	0.20	0.43

Table 5: Temporal dependences of annual wood growth: multiple regression estimates. The data have been centred and scaled. GPP_{gp} is the GPP of the growth period, WS_per_{gp} is the water stress index of the growth period, WS_int_{y-1} is the water stress index of the previous year, and $templim_{gp}$ is the low temperature index of the growth period (see Table 2). D1 and D2 are dummy variables (D1 = 0 if $GPP_{gp} < 1400$ gC m^{-2}; otherwise, D1 = 1. D2 = 0 if $GPP_{y-1} < 1550$ gC m^{-2}; otherwise, D2 = 1; see Fig. 5). The term is the parameter of the first-order autoregressive process that was used to model the temporal autocorrelation of the within-stand errors. Values: estimates [F values]. Estimated values that are significantly different from 0 are indicated (* indicates P < 0.05, ** indicates P < 0.01, and *** indicates P < 0.001). A Δ index indicates that the variable was not retained in the bootstrap procedure (see main text).

All of the explanatory variables had significant effects, but templim was not retained in the models for temperate oaks after the bootstrap procedure that accounted for the uncertainty of the C flux simulations. We observed significant changes in the slopes of the effect of GPP_{y-1} on temperate oaks and the effect of GPP_{gp} on *P. abies* (Table 5). The models with NPP_{gp} and NPP_{y-1} variables revealed the same AWBI dependences as the models described above, but with reduced explanatory power. The models with Ra_{gp} and Ra_{y-1} variables were not significant (data not shown).

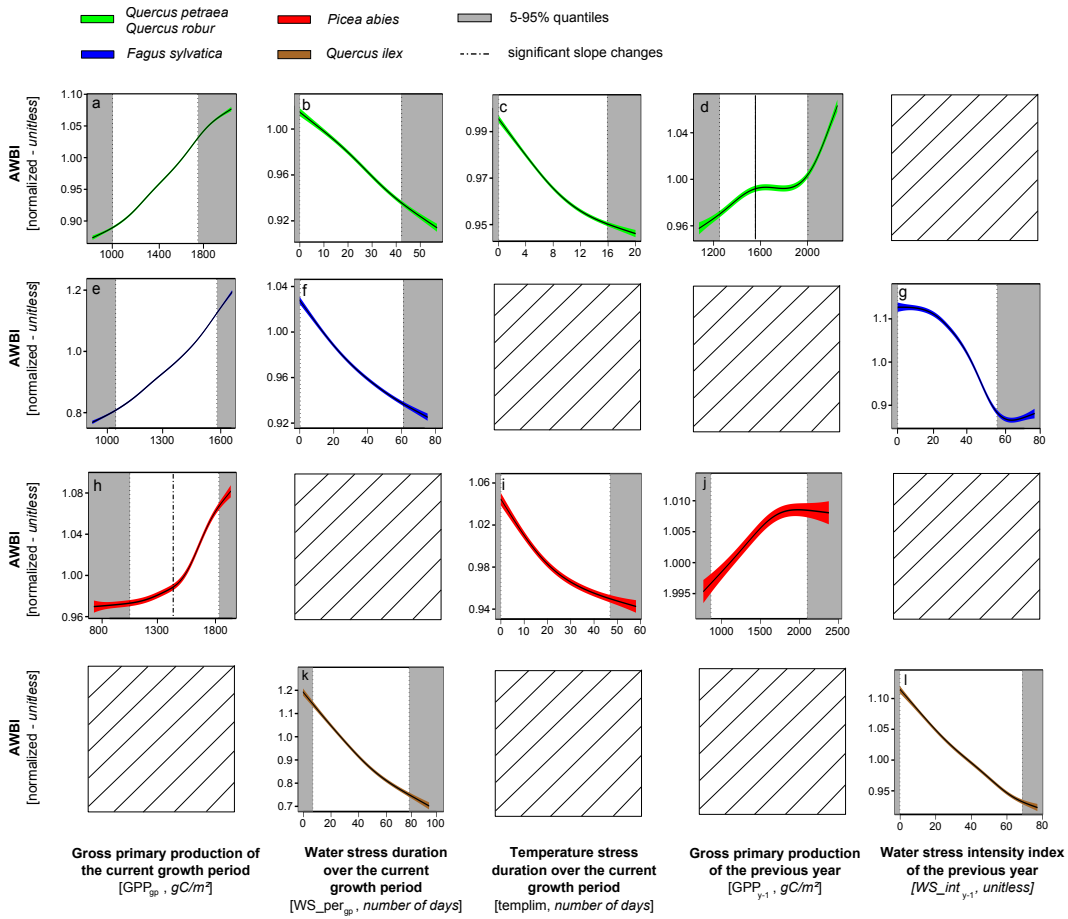

Figure 5: Temporal dependences of annual wood growth: marginal effects of each explanatory variable on the annual wood growth. The lines represent smoothing splines with 50% frequency response cut-offs. The coloured areas indicate the 95% confidence intervals. The 5% and 95% data quantiles (grey areas) were not considered in the discussion. The marginal effect of a given variable X was obtained by fixing the value of X and averaging the RF predictions over all the combinations of observed values for the other predictors in the dataset (Cutler et al., 2007). The marginal predictions were collected over the entire range of X in the training data using a regular grid.

4 Discussion

This study quantified the C that is allocated annually to the woody biomass increment for five species that are representative of the main European forest biomes. By complementing field measurements from a permanent plot network with process-based modelling, our approach circumvented the limitation of EC data scarcity and characterized the annual partitioning of C into woody biomass at 49 sites over France (931 site-years). We were thus able to identify the species-specific drivers of the spatiotemporal dynamics of the allocation of C to wood growth along ecological gradients.

4.1 The correlation between the tree C balance and woody biomass growth

Relating EC-based estimates of forest C balance and biometric measurements of woody biomass growth has been the focus of an increasing number of studies. These studies can enhance our understanding of ecosystem C dynamics but have so far provided conflicting conclusions. Indeed, the correlation between woody biomass growth and forest C gain has been reported as both non-significant (Mund et al., 2010; Richardson et al., 2013; Rocha et al., 2006) and highly significant (Babst et al., 2014; Ohtsuka et al., 2009; Peichl et al., 2010; Zweifel et al., 2010). Accordingly, the relationships between AWBI and C fluxes reported in this study strongly varied among sites for each of the species studied (Table 3). Nevertheless, the annual woody biomass increment was consistently related to GPP_{gp} and NPP_{gp}, and only marginally to Ra_{gp} for the majority of sites (Table 3). Babst et al. (2014) reported a similar dependence of biomass growth on C fluxes at 5 sites that spanned a wide range of latitude in Europe. The authors attributed this result to a common sensitivity of C assimilation and biomass growth to the water balance. Our results also support the view that biomass growth and tree C balance are under the control of distinct but partially correlated processes (Beer et al., 2007; Fatichi et al., 2014); these processes may or may not induce consistent annual changes, depending on the environmental conditions faced by trees. For *F. sylvatica* and temperate oaks, maximum correlation values corresponded to flux aggregation periods that were consistent with the previously reported phenology of the woody biomass increment (Table 3, Michelot et al. 2012, Supplement S10). Babst et al. (2014) and Granier et al. (2008) similarly reported close relationships between the AWBI and forest C fluxes that were summed until cessation of growth (August/September). The

flux aggregation periods were, however, not related to the timing of wood growth in *Q. ilex* or *P. abies* (Cuny et al., 2012; Lempereur et al., 2015), which indicates that inter-annual variation in the AWBI is not always solely (or even primarily, e.g., *Q. ilex* and *P. abies*) dependent on the C derived from photosynthesis. Specifically, the agreement between the observed annual growth and a short period of C flux aggregation in early summer that was reported for *Q. ilex* corresponds to the effect of growth cessation on the annual biomass increment, which has been attributed to a drought-induced limitation of cambial activity at the Puéchabon site (Lempereur et al., 2015). The processes that underlie the relationship of the long flux aggregation period and the annual biomass increment of *P. abies* may include the effect of late winter temperature on cambium phenology (Rossi et al., 2011). Overall, our results suggest that using growth-flux correlation coefficients when investigating either source limitation of growth or the seasonality of C allocation to woody biomass can lead to misleading conclusions.

4.2 Between-site variability in the C allocation to woody biomass growth is related to ontogeny and competition intensity

We highlighted an age-related decline in the C partitioning to woody biomass in all three species (Fig. 3B). This result had previously been observed in *F. sylvatica* stands using measurements of the main C compartments along a chronosequence (Genet et al., 2010). Several non-exclusive processes can explain this age-related trend. Increases in tree height are associated with increases in the hydraulic resistance of xylem, which may lead to declines in the turgor of living cells and result in potentially negative consequences on cambial activity (Woodruff et al., 2004). This constraint may result in a height-related sink-limitation of growth (Woodruff and Meinzer, 2011), which is consistent with our results. Additionally, life-history traits, such as a greater emphasis on reproduction in older stands, could also be involved. However, the interactions of growth and reproductive mechanisms are still under debate (Hoch et al., 2013; Thomas, 2011) and have yet to be properly represented in TBMs. Only the GPP component of the simulated tree C balance was retained in the final models (Table 4), thereby indicating that an increase in maintenance respiration with greater stand biomass most likely did not contribute to the age-related decline in biomass growth (Drake et al., 2011a; Tang et al., 2014). Although height-related hydraulic constraints on C assimilation have been suggested to be an important driver (Ryan et al., 2006; Tang et al., 2014), recent studies have suggested that changes in demography and stand structure

may primarily explain the age-related decline observed in stand wood growth (Binkley et al., 2002; Xu et al., 2012). Our results suggest that changes in the C allocation should also be considered, because no mortality occurred in our plots during the measurement period (data not shown). We additionally identified a significantly higher C partitioning to woody biomass in temperate oak stands with greater competition intensity (i.e., high stand basal area, Table 3). To date, reports regarding the effect of competition on C allocation dynamics are conflicting (Litton et al., 2007) and suggest no significant or consistent effect. Moreover, we found no significant effect of soil nutrient availability on the C allocation dynamics along the studied ecological gradient whereas a recent meta-analysis reported that this factor positively affects C partitioning to forest biomass on the global scale (Vicca et al., 2012). The RENECOFOR network only includes relatively fertile sites (Supplement S5), which could putatively explain the apparent tension between our results and the conclusions of the meta-analysis. Therefore, more studies are required to elucidate the contributions of the various drivers to the variation in C partitioning to woody biomass on scales that range from local to global.

4.3 Inter-annual variability in woody biomass growth is consistent with combined source-sink limitations

Water and temperature stress exerted significant direct control on the inter-annual variation of woody biomass growth (i.e., independently from their effects on C assimilation) for every species and biome (Table 5 and Fig. 4 and 5). Cambial growth has been reported to be inhibited at lower water stress levels than photosynthesis (Muller et al., 2011; Tardieu et al., 2011). Indeed, drought-induced decrease in cell turgor strongly affects cell divisions (Woodruff and Meinzer, 2011) and cell wall expansion (Cosgrove, 2005; Lockhart, 1965) before gas exchange modulation comes into play. Similarly, there is evidence that cell growth processes, such as cell division, are more sensitive than photosynthesis to low temperatures (Körner, 2008). Although these findings documented the plausible mechanisms of sink control of biomass growth at the cellular scale, there is still considerable debate regarding whether the sink or the C source actually limit the growth of the world's forests (Palacio et al., 2014; Wiley and Helliker, 2012). The typically observed large C reserve pools (Hoch et al., 2003; Würth et al., 2005) have been interpreted as a consequence of an overabundant C supply and thus evidence of sink control of tree growth (Körner, 2003). However, recent works have suggested that a source limitation of growth may

be compatible with large C reserve pools if part of this mobile C is sequestered rather than stored (Millard and Grelet, 2010) or if C storage is an active tree response to environmental stress (Dietze et al., 2014; Wiley and Helliker, 2012). Using an alternative methodology (i.e. a methodology that is not based on C storage measurement) our results suggest that sink limitation has a significant effect on the annual woody biomass growth of five species that are representative of different European biomes, including deciduous temperate forests. Because sink limitation implies that there are periods with significant C supply but no growth, our results also corroborate recent empirical studies that reported a significant role of growth duration in the annual variability of tree radial increment (Brzostek et al., 2014; Cuny et al., 2012; Lempereur et al., 2015). Additionally, we observed that past environmental constraints significantly affected C partitioning to wood growth for each species and biome (Table 5 and Fig. 4 and 5). The lagged effect of the previous year's low C supply ($GPP_{y\text{-}1}$) possibly indicates a preferential C allocation to storage at the expense of growth in trees that face C reserve pool depletion (Bansal and Germino, 2008; Wiley et al., 2013). In support of this finding, Richardson et al. (2012) reported a strong relationship between the AWBI and the EC-based estimate of the previous year's C supply in a mature maple stand. The detrimental effect of a previous year's low C supply on temperate oak wood growth (Fig. 4) may be related to growth phenology, because this species relies on C reserves to achieve a large part of its annual biomass growth prior to leaf expansion in the spring (Barbaroux et al., 2003). The lagged effect of high water stress intensity on *F. sylvatica* and *Q. ilex* (Fig. 4) may be linked to previous drought-induced mortalities of buds or fine roots (Leuschner et al., 2001; López et al., 2003). Indeed, pre-built buds are thought to strongly regulate the following year's cambial activity (Delpierre et al., 2015; Palacio et al., 2012; Zweifel et al., 2006) and a recent meta-analysis concluded that C is preferentially allocated to fine roots at the expense of wood growth in stands that face constraining environments (Chen et al., 2013). Finally, our results suggest that C supply (GPP_{gp}) is an important driver of the annual woody biomass growth in temperate deciduous forests (Daudet et al., 2005). GPP was the component of the simulated tree C balance that was most closely related to the annual variability in growth; this result indicates GPP's important role in explaining the annual variability in the net ecosystem productivity of European forests (Delpierre et al., 2012). Overall, our findings support the premise that forest woody biomass growth is subject to complex control processes that include both source and sink limitations, following Liebig's law: although numerous processes potentially influence wood growth, stand growth at a given site and a given

year is predominantly limited by the most constraining factor. C (source) limitation of growth can thus only occur when other factors are non-limiting (Fatichi et al., 2014), a situation that is expected to be rare in strongly constrained environment such as Mediterranean or mountainous areas (Fig. 4).

4.4 Toward an integrated modelling framework

Most models that are currently used to project the outcome of global changes on forests represent wood growth as a fraction of the total C uptake (i.e., source control of growth, De Kauwe et al. 2014). This C-centric perspective overlooks the possibility of sink control of growth and thus ignores results such as those presented in this study and those of earlier local studies (reviewed by Fatichi et al. 2014). Consequently, this perspective possibly hampers the ability of TBMs to project future forest productivity (Fatichi et al. 2014). On the basis of our analysis of the spatiotemporal dynamics of C allocation to wood growth on a regional scale, we suggest a straightforward, combined source- and sink-driven forest growth modelling framework (Fig. 6). In this framework, a potential site-specific allocation coefficient is first defined to represent the effect of soil fertility on the C allocation to wood (Vicca et al., 2012). In a second step, this coefficient is adjusted to the physiological state of the stand by accounting for the dependences of the C allocation on ontogeny, competition intensity and lagged environmental stressors. Lagged environmental stressors are represented by a negative effect on the previous year's water stress index and low C uptake on the allocation coefficient. The resulting potential allocation coefficient is finally modulated on a daily basis by i) the phenology of wood growth, which defines the onset and cessation of the growth period (Delpierre et al., 2015) and ii) the sink limitations of wood growth: the coefficient value of a given day is calculated using the potential coefficient value and the water and temperature stresses experienced during that day. The water and temperature stresses induce day-to-day fluctuations in the allocation coefficient value that represent the sink limitations of wood growth, i.e. the direct effect of water and temperature stresses on growth. The framework presented here is a calibration strategy that requires field data to be implemented in TBMs. Our results can help defining the forms of the coefficient dependences that will be formalized in the next generation of models (Figs. 3 and 5).

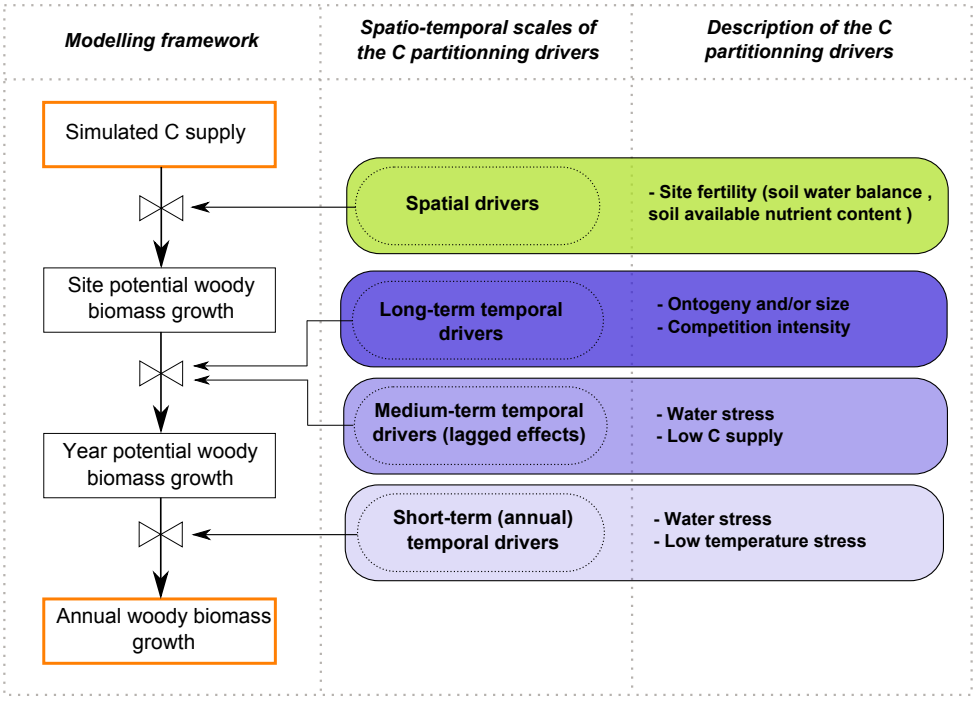

Figure 6: Modelling framework for a combined source- and sink-driven representation of C allocation to wood growth.

Our approach can be seen as an intermediate step toward a more mechanistic representation of C allocation to woody biomass (Hölttä et al., 2010; Schiestl-Aalto et al., 2015). It synthesizes the current knowledge regarding forest growth dependences and has the potential to unify seemingly contradictory observations within a single modelling framework. The simulated growth is indeed subject to the combined controls of C supply and changes in C allocation due to endogenous adjustments and/or modulations of sink activity (Fig. 6). These controls result from distinct processes, which are independently represented in the modelling framework. The relative influences of the various processes, i.e., the simulated growth causalities, are thus likely to vary both spatially and temporally, depending on the environmental conditions faced by trees. Our approach has therefore the potential to shed light on the contrasted results reported by correlative studies. Although the value is comparable to those of previous studies (Lebourgeois et al., 2005; Mérian et al., 2011), the proportion of the annual growth variability that was explained by our approach was moderate (Table 5). Plausible explanations of this result include: i) unreported management interventions that may have skewed the historical stand growth reconstruction and ii) potentially important growth drivers that were not considered here, such as changes in C partitioning due to mast seeding (Mund et al., 2010), genetic differentiation among tree populations (Vitasse et al., 2014) or allometry-mediated tree acclimation to drought

(Martin-StPaul et al., 2013). A third factor that hampered the ability of our empirical models to explain the annual growth variability is the potential disagreement between the CASTANEA outputs that were used as explanatory variables and the corresponding actual drivers. Although we argued that i) the CASTANEA model has been thoroughly validated at many EC sites from throughout Europe and ii) the presented growth dependences demonstrated their robustness against the reported uncertainties of the CASTANEA simulations, the quality of the simulations was limited by the idiosyncrasies of the sites we examined in this study. In particular, a number of past disturbances such as insect outbreaks, windthrow or unreported commercial thinning could have temporarily induced large discrepancies between the actual and simulated C fluxes (Grote et al., 2011; Hicke et al., 2012). The error that is attributable to model performance unfortunately remains unknown because of the absence of EC measurements at our study sites (except for the Puéchabon site, see Delpierre et al., 2012). Despite this additional uncertainty, the combined use of field measurements and process-based modelling allowed us to present the first species-specific evaluation of annual C allocation to growth along regional environmental gradients. Our results suggest that implementing the presented C allocation dependences in TBMs will refine the projections of the outcome of global changes on forest growth, and have implications for the predicted evolution of forest C sink, forest diebacks and tree species distributions (Cheaib et al., 2012).

5 Supplementary data

5.1 Site description

A complete description of the 49 sites used in the study is available in Table S1.1.

ID	Lat. (N)	Long. (E/W)	Elev. (m)	Slope %	Exp.	LNC	Age (year)	SWHC (mm)	H (m)	LAI	ETP (mm)	Prec. (mm)	T (°C)	SNA	period (nb. of years)
F 03	46° 11'	2° 59' E	590	15	N	28.3	87	155	29	6.6	1079	778	10.5	2	1994-1970 (25)
F 04	44° 07'	5° 47' E	1300	50	N	26.7	85	180	25.5	6.6	1328	917	11.6	1	1994-1983 (12)
F 09	42° 55'	1° 16' E	1250	32	SW	26.3	152	110	21.8	4.6	1069	1068	11.5	3	1994-1964 (31)
F 14	49° 10'	0° 51'W	90	0	-	25.3	83	83	25.7	6.2	859	892	10.8	3	1994-1976 (19)
F 21	47° 48'	4° 51' E	400	3	NE	23.5	128	80	28.6	4.3	966	934	9.7	1	1994-1975 (20)
F 26	44° 55'	5° 17' E	1320	12	W	28.3	158	80	80	4.3	1106	1364	6.8	1	1994-1973 (22)
F 52	47° 47'	5° 04' E	440	0	-	25.2	106	100	30.2	5.9	947	987	9	1	1994-1973 (22)
F 54a	48° 30'	6° 42' E	325	5	E	27.1	95	120	29.1	6.2	888	1038	9.5	3	1994-1972 (23)
F54b	48° 38'	6° 04' E	390	2	-	26.3	99	60	28.3	6.2	885	823	9.8	1	1994-1981 (14)
F 55	49° 11'	5° 00' E	250	0	-	25.8	88	150	29.4	5.9	1000	965	9.6	3	1994-1980 (15)
F 60	49° 19'	2° 52' E	138	0	-	26.6	62	160	26.8	6.6	920	717	10.1	2	1994-1982 (13)
F 64	43° 08'	0° 39 W	400	44	NW	26	67	137	28.8	5.3	1064	1299	12.7	2	1994-1977 (18)
F 65	43° 01'	0° 26' E	850	25	NW	29.1	160	180	180	6.4	1080	1114	11.6	2	1994-1972 (23)
F 76	49° 42'	1° 19' E	210	0	-	24.5	87	90	29.9	6.5	776	930	9.9	2	1994-1974 (21)
F 81	43° 24'	2° 10' E	700	0	-	28.1	108	140	30.3	6.3	1219	1102	9.9	2	1994-1972 (23)
F 88	48° 06'	6° 14' E	400	3	W	27.5	68	100	25.4	5.9	877	1092	9.1	3	1994-1983 (12)
Qr 77	48° 27'	2° 42' E	80	0	-	24.3	113	150	27.8	6.1	1009	719	10.7	2	1994-1985 (10)
Qr 18	46° 49'	2° 34' E	175	2	NW	26.9	58	180	17.7	4.6	1031	782	11	2	1994-1987 (8)
Qr 40	43° 44'	0° 50' W	20	5	NE	25.2	46	140	25	5.6	1049	1010	13	1	1994-1984 (11)
Qr 49	47° 27'	0° 01'W	57	0	-	29.1	70	170	28.1	6.9	1085	665	11.5	1	1994-1983 (12)
Qr 55	49° 01'	5° 45' E	220	0	-	23.9	100	150	20.1	5.9	929	827	9.4	1	1994-1972 (23)
Qr 59	50° 10'	3° 45' E	149	3	-	27.2	70	200	22.8	6.5	986	870	9.8	1	1994-1974 (21)
Qr 65	43° 12'	0° 02' W	370	12	SE	25.5	54	160	24.9	4.7	1042	965	12	1	1994-1986 (9)
Qr 71	46° 58'	5° 14' E	190	0	-	26.3	67	190	25.6	6.5	1096	1006	11.3	1	1994-1972 (23)
Qp 01	46° 10'	5° 14' E	260	3	-	23.7	88	170	25.9	6.5	1015	1017	10.5	1	1994-1982 (13)
Qp 03	46° 40'	2° 43' E	260	0	-	27.4	115	100	30.5	5.6	1080	802	10.5	2	1994-1965 (30)
Qp 10	48° 17'	4° 27' E	160	0	-	22.9	83	200	24.9	6.3	1010	778	10.4	1	1994-1987 (8)
Qp 18	47° 15'	2° 07 W	176	1	-	26.3	78	150	28.2	5.9	1025	792	10.9	2	1994-1978 (17)
Qp 27	49° 21'	1° 03' E	175	0	-	27.2	55	170	23.4	6.5	844	768	9.8	2	1994-1984 (11)
Qp 35	48° 10'	1° 32' W	80	0	-	26.3	101	120	29.3	6.1	893	764	11	2	1994-1966 (29)
Qp 41	47° 34'	1° 15' E	127	0	-	25.6	92	180	28.1	5.9	985	639	10.9	3	1994-1972 (23)
Qp 51	49° 01'	4° 57' E	180	2	S	25.4	139	80	25.2	5.9	969	877	9.9	3	1994-1964 (31)
Qp 57a	48° 52'	6° 28' E	320	4	NE	25.1	85	150	27.7	5	1009	719	10.7	1	1994-1970 (25)
Qp 57b	49° 00'	7° 27' E	320	15	NW	20.9	128	140	28.7	5.6	1009	719	10.7	3	1994-1964 (31)
Qp 58	46° 58'	3° 39' E	270	7	SW	24.1	66	150	23.5	6.2	1088	928	10.8	2	1994-1983 (12)
Qp 60	49° 23'	2° 17 W	55	1	-	26.5	60	140	25.3	6.5	855	674	10.2	1	1994-1979 (16)
Qp 61	48° 31'	0° 40' E	220	5	SE	25.8	88	110	26.9	6.7	889	773	10.1	2	1994-1981 (14)
Qp 68	47° 41'	7° 28' E	256	0	-	27.9	137	80	22	5.6	891	811	10.1	3	1994-1970 (25)
Qp 72	47° 46'	0° 22' E	170	0	-	22	64	170	24.1	5.9	952	719	10.9	3	1994-1987 (8)
Qp 81	44° 02'	1° 44' E	300	18	SE	22.1	98	100	27.8	5.3	1246	869	12.0	2	1994-1972 (23)
Qp 86	46° 37'	0° 29' E	116	4	NW	24	82	80	25.1	6.0	1121	758	11.5	3	1994-1985 (10)
Qp 88	48° 01'	6° 02' E	330	0	-	24.8	129	200	26.4	5.7	877	1103	8.99	2	1994-1964 (31)

Table S1.1: Description of the studied sites. ID letters indicate species (F: Fagus sylvatica ; Qr : Quercus robur, Qp : Quercus petraea, P : Picea abies, Qi : Quercus ilex). Lat.: Latitude, Long. : Longitude, Elev. Elevation, Exp.: Exposure, LNC: leaf nitrogen content (gN.gDM-1), SWHC: soil water holding capacity, H: dominant height in 1994, LAI: leaf area index (unitless), ETP: potential evapotranspiration (calculated using the Penman-Monteith equation on a daily basis) , Prec.: precipitation, T: temperature, SNA: soil nutrient availability classes (1=high, 2=medium, 3=low nutrient availability), period: dates and number of available AWBI measurements. ETP, Prec. and T are averaged annual values.

ID	Lat. (N)	Long. (E/W)	Elev. (m)	Slope %	Exp.	LNC	Age	SWHC (mm)	H (m)	LAI	ETP (mm)	Prec. (mm)	T (°C)	SNA	period (nb. of years)
P 39a	46° 11'	2° 59' E	970	10	SE	14	58	90	30.4	6.9	942	1865	7.5	1	1994-1973 (22)
P 39b	44° 07'	5° 47' E	1210	8	W	12.9	111	80	23.6	5.4	931	2100	5.7	1	1994-1979 (16)
P 71	42° 55'	1° 16' E	600	20	SE	13.1	48	100	27	5.8	1055	936	9.8	3	1994-1980 (15)
P 73	49° 10'	0° 51'W	1700	40	NW	12.7	182	110	22.7	4.2	869	1263	4.1	2	1994-1979 (16)
P 74	47° 48'	4° 51' E	1200	20	W	13.8	73	150	30	8.4	939	1737	7.2	2	1994-1978 (17)
P 88	44° 55'	5° 17' E	660	20	SW	14.2	89	100	35.5	6.1	867	1458	8.5	2	1994-1980 (15)
Qi 34	43° 44'	3° 35' E	270	0	-	12	68	113	6	2.4	1417	907	13.4	-	2008-1966 (43)

Table S1.1. *Continued*: Description of the studied sites.

5.2 Reconstruction of the historical circumference trajectories

The historical circumference (CBH) trajectories were obtained on the 49 studied plots by combining forest inventories and tree-ring series. Dendrochronological sampling was conducted after the completion of the forest inventories (Figure S2.1), so that the calculation of historical CBHs inventories could rely on tree-ring series information. 30 trees were cored in the RENECOFOR network (Lebourgeois 1997) and 12 were cored in the Puechabon site (J.M. Ourcival, unpublished data). Past CBH was annually calculated from the initial forest inventory backward. Reconstruction stopped when a sharp decrease of CBH growth indicated non-reported past silvicultural intervention or when the associated stand age felt below 25 years (Figure S.2.1).

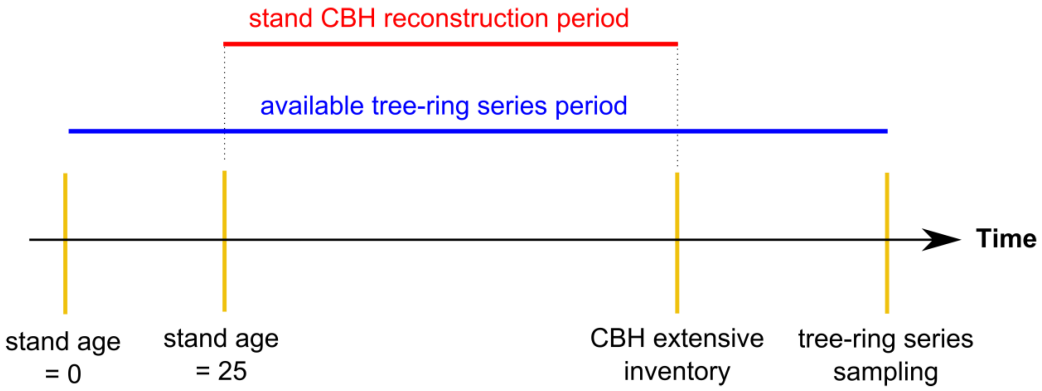

Figure S2.1: Illustration of the growth measurement timing.

First, the CBH trajectories of the cored trees were calculated using tree rings and the CBHs measured at the sampling time. Annual basal area increments were then calculated as follows.

$$BAI_{t,i} = \frac{1}{4\pi}\left(CBH_{t,i}{}^2 - CBH_{t,i-1}{}^2\right) \quad \text{(S2.1)}$$

where $BAI_{t,i}$ is the basal area increment observed on a tree t, in a year i. In a second step, BAI and CBH data were used to calibrate - for each year and each plot - an empirical tree competition model (Deleuze et al. 2004), following the approach described in (Guillemot et al. 2014, Chap. 4). The considered model can be written as follows.

$$BAI_{t,i} = \frac{\gamma_i}{2} \times \left(CBH_{t,i} - m\sigma_i + \sqrt{\left(m\sigma_i + CBH_{t,i}\right)^2 - 4\sigma_i \times CBH_{t,i}}\right) \quad \text{(S2.2)}$$

where $\mathrm{CBH}_{t,i}$ is the circumference at breast height of a given tree t in a year i, and $\mathrm{BAI}_{t,i}$ is its corresponding annual basal area increment. and are the annually calibrated parameters. In this model, only trees with a circumference at breast height (CBH) above the threshold σ_i, which can be interpreted as the minimum circumference for direct access to sunlight, have a significant growth. Overstory trees then grow proportionally to their sizes, following a slope coefficient γ_i (Fig. S2.2). m is a smoothing parameter.

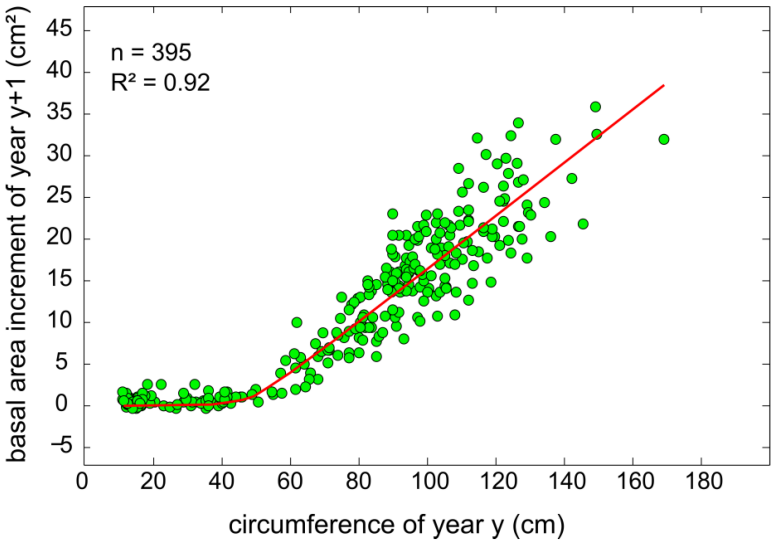

Figure S2.2: Illustration of the tree competition model described in Eq. S2.2. Data were obtained from extensive inventories lead in 2000 and 2009 in plot F03 (Guillemot et al. 2014, Chap. 4).

The calibrated model was then used to infer the BAIs of all the trees of the initial CBH stand distribution. The whole calculation followed an algorithm displayed in Figure S2.3.

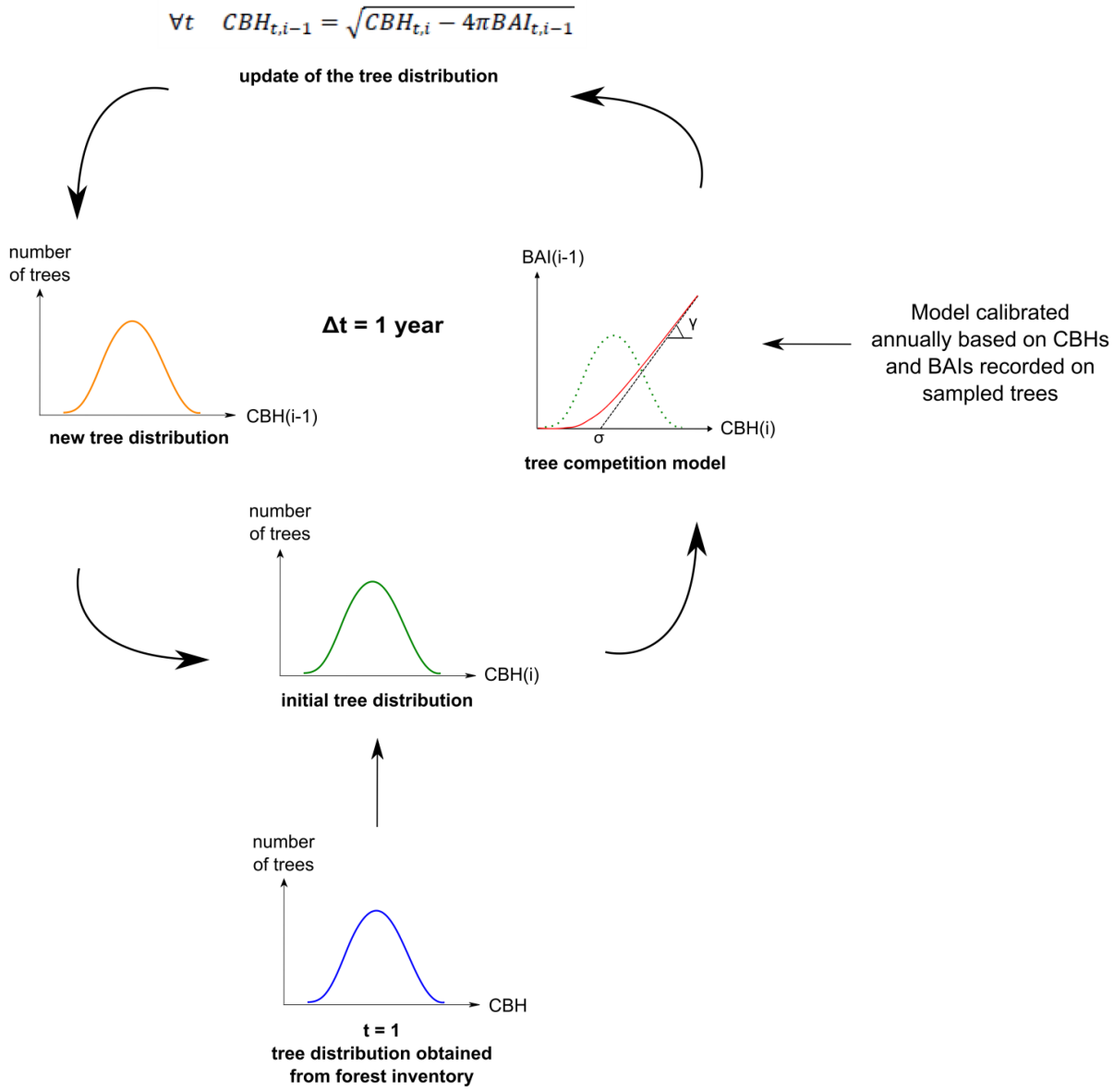

Figure S2.3: Illustration of the algorithm used to reconstruct historical circumference trajectories.

5.3 Calculation of the woody biomass

Supplement 3. Functions used in the calculation of woody biomass Tree woody biomass calculation was based on distinct procedure for *F. sylvatica*, *Q. petraea* and *P. abies* on one hand, and *Q. ilex* on other hand.

5.3.1 F. sylvatica, Q. petraea and P. abies

Top height

- *F. sylvatica* curves

We used the curves suggested by Bontemps, Hervé & Dhôte (2009) which account for the long-term forest productivity trend induced by global changes. The dominant height at the age t, H_t (m), is described as follows.

$$H_t = m1.\exp\left(-\left(pf.m2.chprod(date_0 + t) + \left(ln\left(\frac{a}{H_{t-1}}\right)\right)^{-\frac{1}{m3}}\right)^{-m3}\right) \quad \text{(S3.1)}$$

with

$$\begin{cases} if\ 1900 < date < 2000\ then\ chprod(date) = 1 + m4.(date - 1900) + m5.(date - 1900)^2 \\ if\ date \leq 1900\ then\ chprod(date) = 1 \\ if\ date \geq 2000\ then\ chprod(date) = chprod(2000) \end{cases} \quad \text{(S3.1bis)}$$

- *Q. petraea* curve

Similarly, the curve suggested by Bontemps et al. (2012) also includes explicitly the changes in forest productivity.

$$\frac{dH}{dt} = f2(t - t_b).p_f.f1(H) \quad \text{(S3.2)}$$

where H is the top height (m), t is date, t_b is a reference date (here t_b=1900).

$$f1(H) = \frac{(\frac{H}{K_s})^{m1.m2}}{(1 - m1 + m1(\frac{H}{m3})^{m2})} \quad \text{(S3.2)}$$

$$f2(t) = 1 + d1.u + d2.u^2 + d3.u^3 + \sum_{k=1}^{4} p_k.max(u - 20.k, 0)^3 + \sum_{k=0.}^{1} pm_k.min(u - 20.k, 0)^3 \quad \text{(S3.4)}$$

with $u = t$ - *1900*

- *P. abies* curve

We used the curve suggested in Seynave et al. (2005).

$$H_{age} = m1.\exp\left(-\frac{\left(age.p_f.exp\left(\left(1+\frac{1}{m2}\right).\left(1-ln\left(1+\frac{1}{m2}\right)\right)\right)\right)}{\left((m1.m2)+\left(ln\left(\frac{m1}{1.3}\right)\right)^{\frac{-1}{m2}}\right)^{-m2}}\right) \quad \text{(S3.5)}$$

where H_{age} is the stand dominant height (m) at the corresponding age.

- Parameterization and initialization

The parameterization of Eq. S3.1, S3.3 and S3.5 are provided in Table S3.1.

Species		Parameter values
F. sylvatica	Eastern France	m1=68.7; m2=0.028; m3=0.823; m4=2.03.10^{-3}; m5=3.96.10^{-5}
	Western France	m1=44.2; m2=0.032; m3=1.647; m4=1.245.10^{-3}; m5=1.74.10^{-5}
Q. petraea		K_s=6.1; m1=0.138; m2=2.36; d1=0.2.10^2; d2=0.027.10^3; d3=-0.063.10^4; p1=0.284.10^4; p2=-0.622; p3=1.076; p4=-1.545; pm0=0.024; pm1=-0.076
P. abies		m1=50.7; m2=1.08

Table S3.1: Parameterization of the top height models.

F. sylvativa and *Q. petraea* curves require initialization, defined as follows: $H_{age=0} = 0.3$m. The parameter pf in Eq. S3.1, S3.2 and S3.5 is the site-specific fertility parameter. pf values have been defined by calibrated the curves on height and age measurements. The resulting curves are displayed in Figure S3.1.

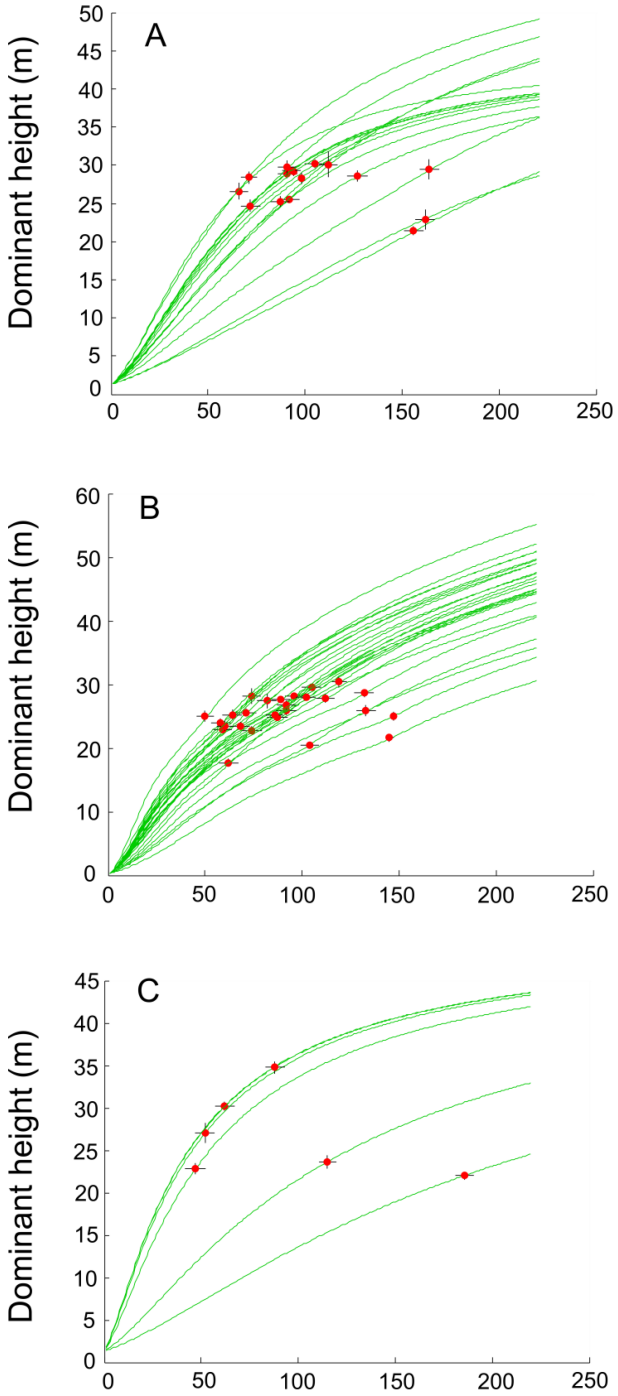

Figure S3.1: Site-specific top height curves for F. sylvatica (A), Q. petraea (B) and P. abies (C). Points and error bar correspond to age and height measurements.

Individual height

The height of each tree is then calculated using the hyperbolic model suggested by Dhôte and de Hercé (1994):

$$H = 1.3 + \frac{((H_0 - 1.3 + p_2.CBH) - \sqrt{H_0 - 1.3 + p_2.CBH)^2 - 4.p_3.p_2.(H_0 - 1.3).CBH}}{2.p_3} \quad \text{(S3.6)}$$

where H is the height of a given tree with a circumference CBH and H_0 is the stand dominant height. p2 and p3 parameters were defined per plot using height and CBH measurements.

Individual above ground volume equations

$$V = form \frac{1}{40000\pi} CBH^2.H \quad \text{(S3.7)}$$

Tree above-ground volumes were calculated from CBH and H, using the equations established by Vallet et al. (2006):

where V is the total above ground tree volume and

$$form = (\alpha + \beta.CBH + \gamma.hdn)(1 + \frac{\delta}{CBH^2}) \quad \text{(S3.8)}$$

with hdn = $CBH^{1/2}$/H. Parameterization of Eq. (S3.8) is provided in Table S3.2.

Parameter	*Q. petraea*	*F. sylvatica*	*P. abies*
α	0.471	0.395	0.631
β	-0.000345	0.000266	-0.000946
γ	0.377	0.421	0
δ	0	45.4	0

Table S3.2: Parameterization of the top height models.

Wood density models

Wood density models typically relates the density of a tree ring formed in year i (WD_i) to tree age (age_i) and ring width (RW_i) (Guilley, Hervé & Nepveu 2004; Bergès, Nepveu & Franc 2008). We used density models established by:

- Zhang et al. (1993) for *Q. petraea*, with WD models as

$$WD_i = \frac{a+b.age_i-(\frac{c}{RW_i})-(\frac{d.age_i}{RW_i})}{1.235} \quad \text{(S3.9)}$$

- Bouriaud et al. (2004) for *F. sylvatica*, with

$$WD_i = \frac{a-b.age+\frac{c}{RW_i}}{1.3} \quad \text{(S3.10)}$$

- Wilhelmsson et al. (2002) for *P. abies*

$$WD_i = a + e.(\ln(age))^b - c.\frac{RW_i}{age \times T_{sum}} + \frac{d.Tsum}{\frac{1}{2}.\frac{RW_i}{age}+2.3} \quad \text{(S3.11)}$$

with

$$T_{sum} = 4922.1\text{-}60.367*48\text{-}0.837*1000 \quad \text{(S3.11bis)}$$

Parameterization of equations S3.9, S3.10 and S3.11 is provided in Table S3.3.

Parameter	Q. petraea	F. sylvatica	*P. abies*
a	817.9	789	304.3
b	0.0038	0.86	0.5
c	98.927	0.32	-444.13
d	0.922	-	0.295
e	1.235	1.3	10.4437

Table S3.3: Parameterization of the top height models.

Annual wood density was calculated for all the available dendrochronological tree ring series and use to convert the corresponding annual volume increment in annual dry matter increment.

The dry matter mass was then converted to carbon biomass assuming 50% carbon content in woody tissues (Pignard et al. 2000).

Individual total volume calculation

Total tree woody biomass of all sites was obtained from above-ground biomass using age-related species-specific relationship after checking for no additional effect of stand density and mean tree size (data not shown).

$$\mathrm{TWB} = \mathrm{AWB} + \mathrm{AWB} \times \mathrm{RS(age)}$$

with TBW the total woody biomass, AWB the above-ground woody biomass and RS the root-shoot ratio, function of stand age. We used root-shoot model established by Genet, Bréda & Dufrêne (2010) for *Q. petraea* and *F. sylvatica* and Lehtonen et al. (2004) for *P. abies*.

$$RS(age) = a + b.\exp(c \times age) \tag{S3.12}$$

Parameter	*Q. petraea*	*F. sylvatica*	*P. abies*
a	0.1893	0.183	0.0838
b	0.8295	1.6259	-0.0365
c	-0.0496	-0.3174	-0.01

Table S3.4: Parameterization of the top height models.

5.3.2 Q. ilex

The calculation of AWB for *Q. ilex* benefited from the work of Rambal et al.(2004) conducted on the studied plot (Puechabon site). $\mathrm{AWB_i}$ of a given tree i was related directly to $\mathrm{CBH_i}$ using a relationship calibrated on 10 stems.

$$AWB = 191.6 \times \left(\frac{CBH}{\pi}\right)^{2.171} \tag{S3.13}$$

The Puechabon site is managed as a coppice, with *Q. ilex* stems sprouting from the stumps after cutting. For this reason, root biomass is there much more important than shoot biomass, at least during the first part of the coppice rotation. We assumed consequently no root biomass growth over the studied period in this site and we calculated the corresponding annual woody biomass increments directly from AWB and not from TWB.

5.4 Annual woody biomass increment features

We calculated annual woody biomass increments as follows for the RENECOFOR plots.

$$AWBI_i = TWB_i - TWB_{i-1} \tag{S4.1}$$

where i corresponds to year. For the Puechabon site, AWBIs were calculated as follows.

$$AWBI_i = AWB_i - AWB_{i-1} \tag{S4.2}$$

Characteristics of the calculated AWBIs are presented in Table S4.1. The mean sensitivity and first order auto-correlation coefficient were calculated on detrended data to measure, respectively, the year-to-year variability and the lagged influence of growth of the previous year on the current year growth (Fritts 2012).

ID	R^2 (%)	RMSE ($gC.m^{-2}$)	mean AWBI ($gC.m^{-2}$)	MS (unitless)	AC (unitless)
F 03	*36.8 ± 3.9*	*10.0 ± 1.3*	*379.7*	*0.19*	*0.40*
F 04	*61.6 ± 14.3*	*5.1 ± 2.3*	*267.0*	*0.17*	*0.15*
F 09	*52.0 ± 13.9*	*9.8 ± 0.9*	*158.7*	*0.22*	*0.18*
F 14	*54.2 ± 14.4*	*5.4 ± 1.9*	*262.8*	*0.23*	*0.36*
F 21	*35.0 ± 5.9*	*13.3 ± 1.9*	*204.5*	*0.23*	*0.36*
F 26	*54.0 ± 11.6*	*9.3 ± 0.6*	*160.1*	*0.22*	*0.28*
F 52	*41.6 ± 12.5*	*5.5 ± 1.6*	*273.7*	*0.26*	*0.18*
F 54a	*60.7 ± 16.1*	*9.7 ± 2.4*	*391.1*	*0.23*	*0.16*
F54b	*67.1 ± 11.5*	*7.7 ± 1.9*	*231.3*	*0.21*	*0.29*
F 55	*46.9 ± 17.8*	*9.9 ± 2.0*	*379.0*	*0.12*	*0.20*
F 60	*74.1 ± 18.1*	*6.3 ±1.6*	*405.7*	*0.17*	*0.32*
F 64	*52.4 ± 13.1*	*8.4 ± 2.3*	*415.1*	*0.17*	*0.34*
F 65	*59.3 ± 12.2*	*7.3 ± 1.3*	*237.9*	*0.15*	*0.24*
F 76	*36.5 ± 9.9*	*8.8 ± 1.8*	*278.2*	*0.19*	*0.41*
F 81	*38.8 ± 13.3*	*7.5 ± 1.5*	*279.9*	*0.18*	*0.37*
F 88	*38.9 ± 5.3*	*6.7 ± 1.2*	*381.1*	*0.13*	*0.45*
Qr 77	*42.6 ± 16.1*	*9.7 ± 2.4*	*238.7*	*0.15*	*0.67*
Qr 18	*68.6 ± 6.2*	*3.6 ± 1.3*	*247.2*	*0.17*	*0.20*
Qr 40	*63.5 ± 15.6*	*8.7 ± 1.7*	*351.9*	*0.18*	*0.26*
Qr 49	*44.5 ± 7.0*	*10.8 ± 1.7*	*409.3*	*0.13*	*0.46*
Qr 55	*30.7 ± 10.9*	*7.6 ± 1.8*	*104.0*	*0.15*	*0.23*
Qr 59	*38.0 ± 13.8*	*5.6 ± 1.6*	*228.3*	*0.22*	*0.20*
Qr 65	*77.8 ± 7.5*	*4.9 ± 1.3*	*296.5*	*0.23*	*0.24*
Qr 71	*35.4 ± 1.4*	*6.7 ± 1.6*	*303.4*	*0.17*	*0.25*
Qp 01	*47.0 ± 12.7*	*5.1 ± 1.5*	*264.2*	*0.15*	*0.12*
Qp 03	*70.8 ± 11.9*	*4.3 ± 0.9*	*278.7*	*0.14*	*0.17*
Qp 10	*34.8 ± 7.6*	*7.6 ± 1.6*	*260.9*	*0.12*	*0.28*
Qp 18	*37.9 ± 5.8*	*6.9 ± 1.8*	*370.4*	*0.15*	*0.33*
Qp 27	*87.4 ± 9.1*	*5.4 ± 1.5*	*303.3*	*0.14*	*0.16*
Qp 35	*35.0 ± 10.1*	*6.5 ± 1.5*	*307.4*	*0.12*	*0.22*
Qp 41	*61.8 ± 19.6*	*5.9 ± 0.8*	*276.6*	*0.19*	*0.31*
Qp 51	*73.5 ± 17.0*	*5.9 ± 0.9*	*184.1*	*0.13*	*0.39*
Qp 57a	*57.2 ± 13.9*	*3.8 ± 1.1*	*355.1*	*0.18*	*0.32*
Qp 57b	*77.8 ± 9.5*	*4.8 ± 0.6*	*175.5*	*0.13*	*0.28*
Qp 58	*64.2 ± 9.8*	*6.2 ±0.9*	*345.3*	*0.11*	*0.27*
Qp 60	*63.9 ± 10.3*	*4.7 ±1.1*	*344.9*	*0.19*	*0.15*
Qp 61	*41.9 ± 6.0*	*4.6 ±0.7*	*316.9*	*0.10*	*0.18*
Qp 68	*36.4 ± 4.5*	*7.5 ± 2.0*	*99.7*	*0.18*	*0.11*
Qp 72	*65.6 ± 9.7*	*4.8 ± 1.4*	*370.9*	*0.17*	*0.14*
Qp 81	*54.0 ± 22.4*	*3.7 ± 1.1*	*197.8*	*0.18*	*0.18*
Qp 86	*60.0 ± 11.3*	*6.2 ± 1.2*	*343.1*	*0.19*	*0.25*
Qp 88	*35.2 ± 13.1*	*5.7 ± 1.9*	*209.3*	*0.15*	*0.40*
P 39a	*36.2 ± 18.3*	*10.0 ±2.3*	*472.4*	*0.16*	*0.29*
P 39b	*46.6 ± 10.9*	*5.1 ± 0.9*	*236.2*	*0.14*	*0.32*
P 71	*47.8 ± 14.7*	*9.8 ± 2.5*	*318.5*	*0.20*	*0.34*
P 73	*69.8 ± 15.8*	*5.4 ± 0.8*	*207.8*	*0.15*	*0.31*
P 74	*45.2 ± 14.9*	*13.3 ± 2.0*	*475.7*	*0.16*	*0.35*
P 88	*63.8 ± 12.8*	*9.3 ± 1.6*	*365.6*	*0.13*	*0.31*
Qi 34	*59.3 ± 14.2*	*9.2 ± 1.2*	*101.9*	*0.35*	*0.12*

Table S4.1: Site-specific characteristics of the annual woody biomass increments (AWBI). R^2 and RMSE (coefficient of determination and root mean square error) correspond to the goodness of fit of the tree competition model used in the CBH reconstruction (mean ± standard error), mean AWBI is calculated on raw data, MS and AC are the mean sensitivity and the first-order autocorrelation coefficient of the detrended AWBI series, respectively.

5.5 Classes of soil nutrient availability

ID	C/N	T/S	CEC	SNA
F 03	*14.5*	*9.8*	*4.2*	2
F 04	*13.2*	*99.9*	*29.4*	1
F 09	*14.8*	*13.2*	*5.3*	3
F 14	*15.6*	*9.8*	*4.2*	3
F 21	*15.0*	*99.9*	*42.3*	1
F 26	*11.9*	*99.9*	*39.8*	1
F 52	*13.3*	*99.8*	*30.9*	1
F 54a	*15.0*	*19.9*	*3.4*	3
F54b	*12.6*	*99.7*	*38.3*	1
F 55	*17.7*	*11.9*	*3.0*	3
F 60	*13.0*	*99.9*	*13.7*	2
F 64	*10.5*	*60.7*	*6.6*	2
F 65	*11.3*	*10.5*	*5.3*	2
F 76	*13.7*	*9.0*	*3.3*	2
F 81	*14.2*	*12.9*	*4.4*	2
F 88	*16.2*	*12.6*	*3.8*	3
Qr 77	*14.8*	*34.8*	*1.05*	2
Qr 18	*17.8*	*88.6*	*14.5*	2
Qr 40	*11.6*	*73.8*	*2.75*	1
Qr 49	*10.7*	*39.1*	*1.2*	1
Qr 55	*12.9*	*86.0*	*15.3*	1
Qr 59	*12.7*	*42.1*	*6.5*	1
Qr 65	*10.2*	*26*	*2.8*	1
Qr 71	*14.6*	*54.0*	*4.4*	1
Qp 01	*12.8*	*13.5*	*2.8*	1
Qp 03	*16.8*	*23.9*	*1.5*	2
Qp 10	*13.6*	*23.2*	*5.8*	1
Qp 18	*19.5*	*11.8*	*1.4*	2
Qp 27	*14.9*	*20.1*	*6.3*	2
Qp 35	*15.2*	*7.7*	*2.8*	2
Qp 41	*17.8*	*16.2*	*3.8*	3
Qp 51	*19.7*	*25.9*	*6.7*	3
Qp 57a	*12.0*	*29.1*	*3.9*	1
Qp 57b	*23.6*	*7.5*	*2.0*	3
Qp 58	*14.9*	*29.3*	*3.4*	2
Qp 60	*13.4*	*36.9*	*2.6*	1
Qp 61	*15.8*	*31.3*	*6.8*	2
Qp 68	*16.1*	*21.9*	*3.5*	3
Qp 72	*25.3*	*11.9*	*2.9*	3
Qp 81	*15.9*	*23.2*	*6.2*	2
Qp 86	*26.0*	*12.0*	*2.4*	3
Qp 88	*15.9*	*20.8*	*4.5*	2
P 39a	*10.9*	*98.1*	*26.8*	1
P 39b	*10.9*	*98.1*	*26.8*	1
P 71	*12.3*	*4.5*	*4.0*	3
P 73	*15.7*	*34.5*	*4.0*	2
P 74	*12.4*	*98.1*	*14.1*	2
P 88	*15.3*	*14.3*	*4.0*	2
Qi 34	-	-	-	-

Table S5.1: Soil characteristics of the studied plots. C/N: carbon-nitrogen biomass ratio, T/S: percent base saturation, CEC: cationic exchange capacity, SNA: soil available nutrient classes (1=high, 2=medium, 3=low nutrient availability).

5.6 Species-specific aggregation periods of C fluxes used in the analyses

The period we retained for the aggregation of C fluxes in the present studies was based on reported measurement on species-specific wood growth phenology (Table S6.1).

Species	Start	End	Reference
F. sylvatica	110	270	Skomarkova *et al.* 2006
Q. petraea	90	260	Michelot *et al.* 2012
P. abies	100	300	*H. Cuny, C. Rathgeber, unpublished data*
Q. ilex	130	330	*N. Martin-StPaul, unpublished data*

Table S6.1: Aggregation periods of carbon fluxes. Values are day of the year.

5.7 Physiology-based index of stress water intensity

The CASTANEA model simulates daily the soil water balance, based on a bucket soil sub-model with 2 layers (a top soil layer and a total soil layer, including top soil layer) (Dufrêne et al., 2005). Based on the soil water balance, an index of water stress (reduc, unitless) is calculated daily.

$$reduc_t = \max\left(0, \min\left(1, \frac{SWC_t - SWC_{wilt}}{0.4 \times \left(SWC_{fc} - SWC_{wilt}\right)}\right)\right) \tag{S7.1}$$

where SWC_t is the soil water content of day t (mm), SWC_{wilt} is the soil water content at wilting point (mm) and SWC_{fc} is the soil water content at field capacity (mm). reduc calculation is based on the water stress effect on stomatal conductance (Granier et al. 1999). In addition,

$$reduc_t = 1 \text{ if } SWCtop_t > SWCtopwilt \tag{S7.2}$$

where SWC_{topt} is the soil water content of the top soil layer (mm) and $SWC_{topwilt}$ is the soil water content of the top soil layer at wilting point (mm). This aims to reproduce the positive effect of light rain (only affecting top soil water balance) on stomatal conductance (Dufrêne et al., 2005). Finally,

$$\text{WS\_int} = \sum (1 - reduc_t) \tag{S7.3}$$

where WS_int (unitless) is the physiology-based soil water stress intensity index. In the present study, AWBI has been related to the soil water intensity index summed over the growing period (WS_int_{gp}) and to the to the soil water intensity index summed over the previous year (WS_int_{y-1}).

5.8 Modelling of the biomass growth onset

The growth resumption of *F. sylvatica* is known to occur simultaneously with budburst (Michelot et al. 2012) and we simulated consequently the day of growth biomass onset for this species based on the leaf phenology sub-model of CASTANEA (Dufrêne et al. 2005). For the other species, the day of growth cambial onset was simulated annually using a simple model based on daily temperature and thermic threshold (Rossi et al. 2008, 2011). In this model a thermic forcing variable R_f is calculated daily as follows.

$$R_f(N) = \begin{cases} T \; if \; T(N) \geq T_b \\ 0 \; if \; T(N) < T_b \end{cases} \tag{S8.1}$$

where N is the day of the year, T is the daily average temperature and T_b is a threshold parameter. Then,

$$\begin{cases} S_f(n) = \sum_{N_{start}}^{N} R_f(n) & if \quad S_f(n) < T_{crit} \\ D_{start} = N & if \quad S_f(n) = T_{crit} \end{cases} \tag{S8.2}$$

where S_f is a sum of temperature, T_{crit} and N_{start} are parameters and D_{start} is the day of growth onset. Species-specific parameterization of the growth biomass onset model can be found in Table S8.1.

Species	T_b	N_{start}	T_{crit}	Reference
Q. petraea	1	51	267	David (2011)
P. abies	-2	87	403.9	*N. Delpierre, unpublished data*
Q. ilex	5	1	933	*N. Martin-StPaul, unpublished data*

Table S8.1: Parameterization of the biomass growth onset model.

5.9 Uncertainty of the CASTANEA simulations of carbon fluxes

The capacity of the CASTANEA model to reproduce annual forest C balance has been thoroughly evaluated over Europe (Delpierre 2009). We reported in Table S9.1 the species-specific root mean square error used in the bootstrapp procedure to account for the simulation uncertainty in linear model tests.

		Species			
		F. sylvatica	*Q. petraea*	*P. abies*	*Q. ilex*
RMSE ($gC.m^{-2}$)	GPP	78	104	85	88
	Ra	96	186	201	131
	NPP	60	140	66	59

Table S9.1: Root mean square error (RMSE) of the CASTANEA simulations (Delpierre 2009). GPP: gross primary productivity, Ra: autotrophic respiration, NPP: net primary productivity.

5.10 Seasonal agreement between AWBIs and the components of the forest carbon balance

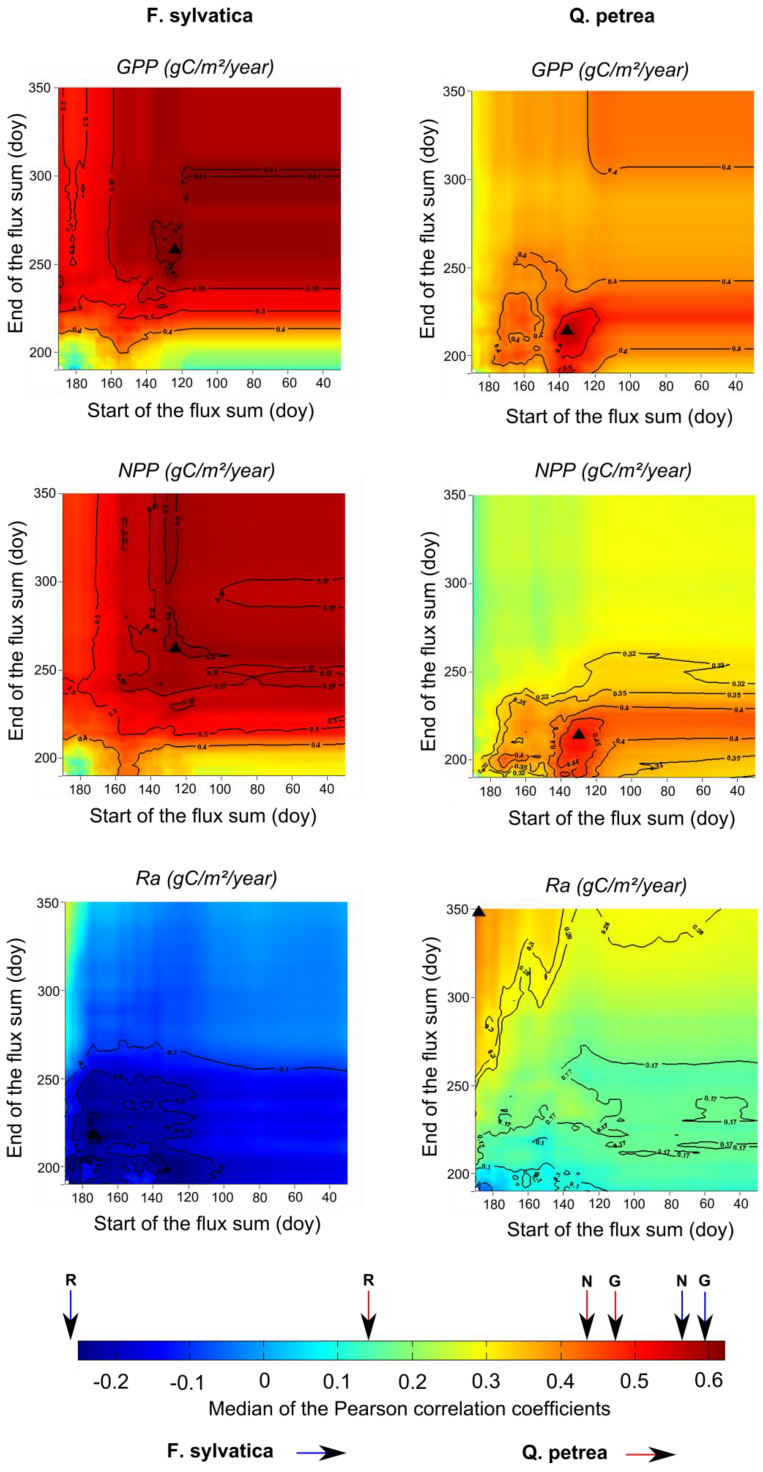

Figure S10.1: Seasonal agreement between AWBIs and the components of the forest carbon balance. Values are the median of the Pearson coefficients estimated on each plot. Triangle marks the maximum median value. Critical values for each flux (G: gross primary productivity, N: net primary productivity, R: autotrophic respiration) are reported with arrows on the color-bar. Critical values outside the color-bar mean that no values differed from the maximum median correlation.

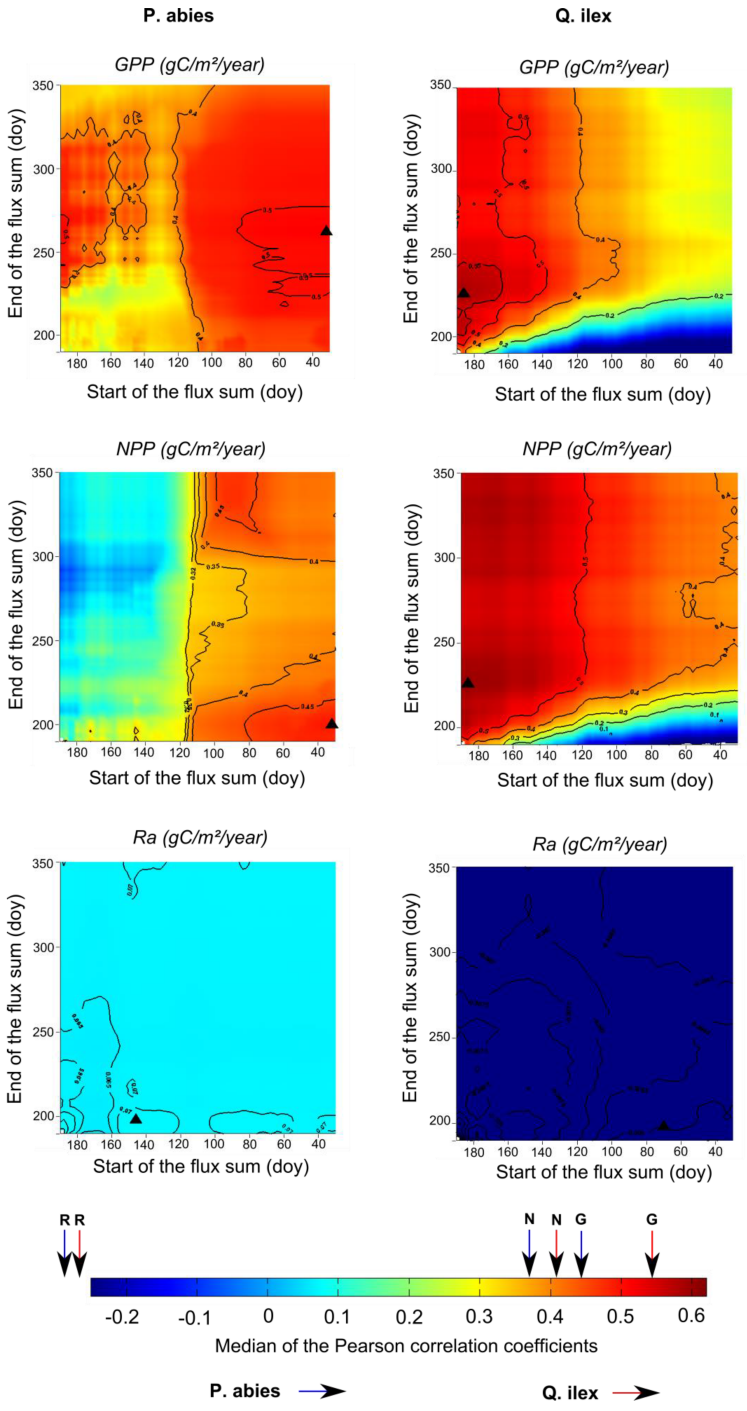

Figure S10.1. *Continued*: Seasonal agreement between AWBIs and the components of the forest carbon balance.

Chapter 3

Environmental control of the sink activity affects the projections of wood growth in European forests

1 Introduction

There is a consensus that tree functioning and survival will be increasingly affected by global changes (Allen et al., 2010; Hartmann, 2011; Bellard et al., 2012). This may translate into deep changes in ecosystem services associated with forests, such as the mitigation of the increase of the atmospheric CO_2 concentration ($[CO_2]$; Ballantyne et al., 2012; Sarmiento et al., 2010) or the supply of timber, with potentially large economic consequences on scales that range from local to global (Hanewinkel et al., 2012). There is therefore a strong need for sound projections of forest productivity in order to define future management policies and silvicultural guidelines (Fontes et al., 2010). However the current projections of forest productivity are flawed by various sources of uncertainty and terrestrial biosphere model (TBM) simulations of forest biomass increment suffer the lack of large scale evaluations (Zaehle et al., 2006; Bellassen et al., 2011b).

Among the different sources of uncertainty, climate change scenarios, model parameters, and model structure are of prominent importance (Schaphoff et al., 2006; Keenan et al., 2012a). The model structural uncertainty arises from an incomplete representation of ecophysiological processes, particularly the processes underlying the long-term ecosystem dynamics (Luo et al., 2011). For instance, the magnitude of the long-term effect of nitrogen limitation on net primary productivity (NPP) under elevated $[CO_2]$ remains controversial (Zaehle & Dalmonech, 2011) and is not fully accounted for in TBMs (Zaehle et al., 2014). Similarly, a complete representation of the acclimation of photosynthesis to elevated $[CO_2]$ is still lacking in most TBMs (Smith & Dukes, 2013). Besides the uncertainty associated with the future of the NPP of forests, the within-tree C allocation may be a major cause of uncertainty in terrestrial C sink projections. The partitioning of C among tree compartments has, together with forest disturbances (Seidl et al., 2014) and demography, an important impact on the residence time of C in forest ecosystem, which is a major uncertainty source in TBMs (Friend et al., 2014). Moreover, the within-tree C partitioning may be a key process involved in the forest diebacks that occur worldwide (McDowell, 2011; Doughty et al., 2015), with potential effects on the future global C cycle (Anderegg et al., 2013).

In particular, the partitioning of C among tree organs determines the dynamic of leaf area index (LAI), a fundamental ecosystem property setting the exchanges of water, carbon and energy between the forests and the atmosphere (Otto et al., 2014). Besides, it has been reported that the reduction of LAI may alleviate the drought stress of trees when water deficit is pursued

over several years or decades (Maseda & Fernández, 2006; Martin-StPaul et al., 2013). LAI is therefore an important variable to consider in TBMs, in the context of increasing water deficit related to climate change (Dai, 2013). In the last decade, the modelling of LAI benefited from satellite-derived observations that were used to prescribe LAI in TBMs, evaluate models and highlight environmental dependences of LAI at regional scale (Soudani et al., 2006; Randerson et al., 2009; Smettem et al., 2013; Chakroun et al., 2014). A better representation of the LAI dynamic in TBMs remain however an important challenge toward accurate C cycle projections (Richardson et al., 2012) and sound regional evaluations of simulated LAI are scarce despite the recent profusion of satellite-derived data (Lafont et al., 2012).

Ultimately, the amount of C allocated to the long-lived tissues, i.e. the above and below-ground wood compartments, will influence the capacity of forests to act as a persistent C sink (Zhang et al., 2010; Pan et al., 2011). Despite recent encouraging advances made on particular sites (Richardson et al., 2013; Li et al., 2014; Gea-Izquierdo et al., 2015; Lempereur et al., 2015; Schiestl-Aalto et al., 2015), TBMs used in regional and global C cycle projections do not perform well at predicting annual wood growth and wood stocks (Babst et al., 2013; De Kauwe et al., 2014). Moreover, recent studies stressed the risk of 'getting the right answers for the wrong reason' (Fatichi et al., 2014) when using the current generation of TBMs for predicting forest wood growth. Most of the TBMs that are currently used to project future global C cycle indeed partition C into different tree compartments using empirical coefficients (Arora et al., 2013; Jones et al., 2013). These coefficients are typically fixed or they vary on a daily basis according to organ-specific phenology or functional equilibriums (Franklin et al., 2012; De Kauwe et al., 2014; Delpierre et al., 2015). In any case, the simulated wood growth is a fraction of the C entering the ecosystem during a given period (i.e., growth is limited by the source of C). This C-centric paradigm has been challenged by empirical evidences reporting that cambial activity is more sensitive than C assimilation to a panel of environmental stressors (Sala et al., 2012; Fatichi et al., 2014), including water deficit (Muller et al., 2011; Tardieu et al., 2011; Lempereur et al., 2015) and low temperatures (Körner, 2008). These experimental reports suggest that the direct control of the C sink by environmental or internal factors could exert a predominant influence on growth (i.e., growth is limited by the sink activity). This is in line with the large amount of total non-structural carbohydrate (TNC) usually found in trees (Körner, 2003), even though recent works suggest that a source limitation of growth may be compatible with large C reserve pools if

a part of this mobile C is sequestered rather than stored (Millard & Grelet, 2010) or if C storage is an active tree response to environmental stress (Wiley & Helliker, 2012; Dietze et al., 2014). Actively stored C reserve could explain the time lags often observed between annual C uptake and biomass growth (Rocha et al., 2006; Richardson et al., 2013) if the C accumulated in reserve is not used until the following year. In a recent evaluation along regional gradients, Guillemot et al., (2015b, Chap. 2) reported that the annual growth of four major European species is consistent with a complex control of C allocation to wood, which involve a C source control and a variety of sink limitations that are currently not implemented in most TBMs (but see Leuzinger et al., 2013). The implications of the sink limitations for the future of forest growth and wood stocks under climate change are yet to be quantified. Sound projections of forest growth at large scale are indeed urgently needed: a part of the terrestrial C sink in the middle and high latitudes of the northern hemisphere has been attributed to a growth enhancement induced by environmental changes (Ciais et al., 2008; McMahon et al., 2010; Fang et al., 2014; Pretzsch et al., 2014). A reversal of this trend may strongly affects the future land-atmosphere feedbacks (Nabuurs et al., 2013).

In this study, we present a new C allocation scheme implemented in the CASTANEA terrestrial biosphere model (Dufrêne et al., 2005). The allocation of C is represented using four compartments competing for C supply on a daily basis and integrates a combined source-sink limitation of wood growth (Guillemot et al., 2015b, Chap. 2). The new version of CASTANEA was calibrated and evaluated on the regional scale using a combination of satellite-derived data, biometric measurement from forest inventories and C storage data from a recent global meta-analysis (A. Sala & J. Martínez-Vilalta, *unpublished data*). The study was conducted for four major European tree species: *Fagus sylvatica*, *Picea abies*, *Quercus ilex*, and a generic temperate oak representing *Quercus petraea* and *Quercus robur*. We finally used the validated model to evaluate how the environmental limitations of the sink activity impacted the simulated changes in European forest growth over the 21st century. The implications of the sink control for the projected growth changes were evaluated relatively to the uncertainty associated with the C emission scenarios and long-term effect of elevated [CO_2] on plant physiology.

2 Materials and methods

2.1 Modelling of carbon allocation

In this study, we relied on the original version of the CASTANEA TBM (Dufrêne et al., 2005), that included subsequent modifications from Delpierre et al., (2009b). The simulations of CASTANEA have been thoroughly validated against eddy-covariance data from throughout Europe (e.g., Davi et al., 2005; Delpierre et al., 2009b). One of the major strengths of the model (Keenan et al., 2012b) is its ability to reproduce the inter-annual fluctuations of the water and C gas exchanges between the forest and the atmosphere (Delpierre et al., 2012). The simulated stand comprised four functional compartments: foliage, woody biomass (that included stem, branches and coarse roots), fine roots and the pool of TNC, i.e., the reserve C pool. In previous versions of the model, the biomass growth of tree compartments was simulated as a fraction of NPP, using seasonally fixed proportions (allocation coefficients, Dufrêne et al., 2005) that responded to functional equilibria (Davi et al., 2009). Here, the C allocation coefficients were determined on a daily basis by the organ-specific phenology, modulations of sink activity by water and low temperature stresses and lagged environmental effects (Fig. 1). The C supply that was allocated on a given day was calculated by subtracting the maintenance C cost of existing biomass (maintenance respiration) to the photosynthesis. The growth respiration was calculated after the C had been partitioned among compartments, as a function of organ-specific growth rates and construction costs (Dufrêne et al., 2005). The values of the model parameters were species-specific.

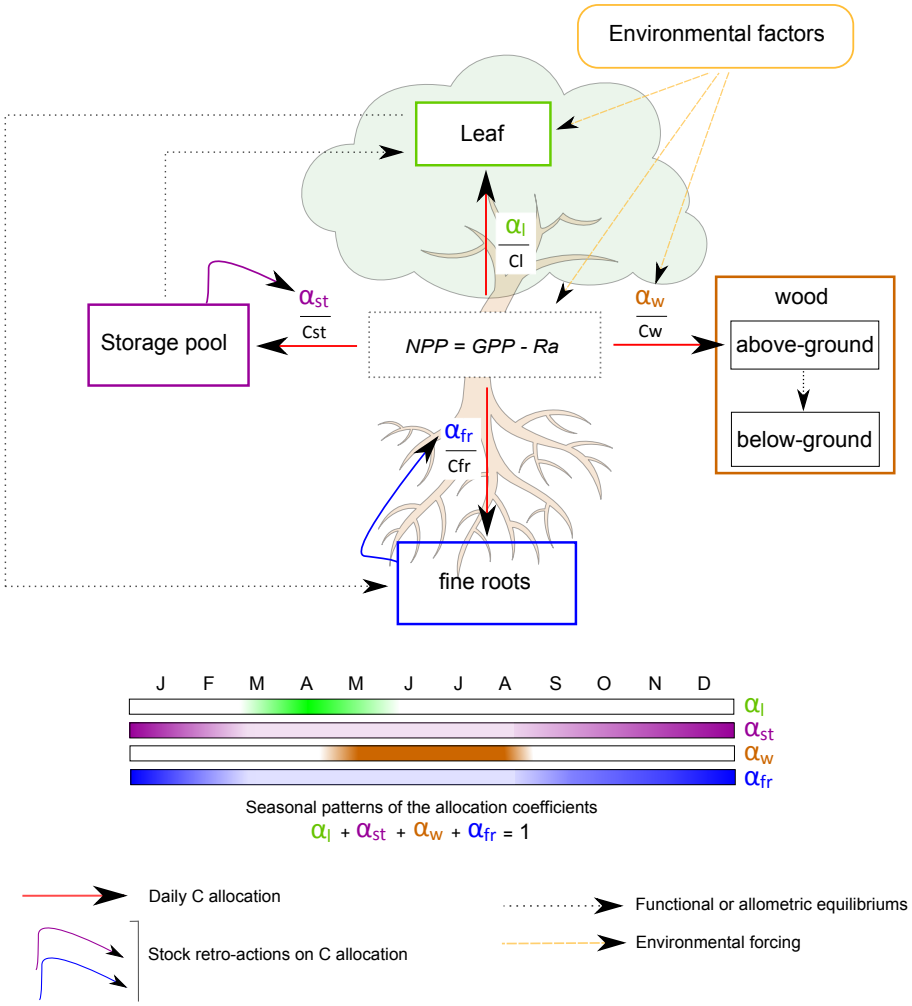

Figure 1: Schematic diagram of the C allocation scheme that was implemented in the CASTANEA model. The symbols correspond to the allocation coefficients. NPP: Net primary production, GPP: Gross primary production, Ra: Autotrophic respiration.

2.1.1 Leaf compartment

The dates of budburst and leaf senescence were simulated using accumulated degree-day, combined to photoperiod sensitivity for the latter (Dufrêne et al., 2005; Delpierre et al., 2009b). The amount of C that was allocated to the leaf compartment strongly relied on the C reserve pool because the stand C balance was negative during most of the leaf formation. During the period of leaf formation, C was allocated to leaf until the simulated LAI reached a defined annual maximum (LAImax). The LAImax was a prognostic variable. The value of the LAImax of the year *n* was determined by i) the LAImax of the year *n-1* and ii) the water stress experienced by the stand during the year *n-1*: LAImax decreased after drought years, but increased otherwise (Eq. 1).

$$\mathrm{LAImax}_n = \min(plai1, \mathrm{LAImax}_{n-1} + (plai2 - plai3 \times SWS_{n-1})) \quad (1)$$

Where LAImax is the annual maximum LAI, SWS_{n-1} is the soil water stress index of year *n-1*, plai1 is the parameter that corresponds to the maximum value possible for LAImax, plai2 and plai3 are the parameters associated with the effect of SWS. The SWS is a bioclimatic index that integrates the water balance and the soil water holding capacity of the site (SWHC). Details about the calculation of SWS can be found in Guillemot et al., (2015b, Chap. 2). The minimum value of the simulated LAImax was fixed to 2.5 for *F. sylvatica*, *Q. petraea* and *P. abies* and to 1.8 for *Q. ilex*. Eq. 1 was used to describe the C allocated to leaf compartment for all the studied species. However, in the case of the evergreen species only the last needle or leaf cohort (out of 6 and 4, for *P. abies* and *Q. ilex*, respectively) was affected by the annual changes in LAImax.

2.1.2 Wood compartment

The annual C allocation to wood was based on the modelling framework described in Guillemot et al., (2015b, Chap. 2). Three versions of the C allocation sub-model were calibrated (Table 1): a null version with a constant allocation coefficient (hereafter 'CST version'), a version that included the age-relative decline in C allocation to wood (hereafter 'STD version') and a full version that additionally included the lagged effect of the previous year's water stress and the sink limitations on wood growth (hereafter 'FULL version').

The allocation coefficient of the CST version was calculated using Eq. 2.

$$WAC_{n,d} = p\mathrm{wood1} \quad (2)$$

Where $WAC_{n,d}$ is the wood allocation coefficient simulated in day *d* of year *n*. pwood1 is a parameter.

In version STD, the simulated allocation coefficient varied annually to account for the age-related decline in C allocation to wood (Eq. 3)

$$WAC_{n,d} = p\text{wood1} - \text{pwood2} \times \text{age} \qquad (3)$$

Where $WAC_{n,d}$ is the wood allocation coefficient simulated in day *d* of year *n*. pwood1 and pwood 2 are parameters.

The FULL version also incorporated the age-related decline in C allocation to wood (Eq. 4) but the resulting WAC value was additionally modulated on a daily basis by i) the negative lagged-effect of previous year's water stress on wood growth (Eq. 5) and ii) the direct environmental control on the sink activity: when the water or the low temperature stresses of a given day exceeded a defined threshold, the sink activity was assumed to temporarily stop and no C could be allocated to wood (Eq. 6).

$$WAC1_{n,d} = p\text{wood1} - \text{pwood2} \times \text{age} \qquad (4)$$

$$WAC_{n,d} = WAC1_{n,d} - \text{pwood3} + \frac{\text{pwood4}}{1 + \exp(\text{pwood5} \times (SWS_{n-1} - \text{pwood6}))} \qquad (5)$$

$$\begin{aligned} &If\ (REW_{n,d} < \text{psink1 or } Ta_{n,d} < \text{psink2}) \quad \text{then} \quad WAC_{n,d} = 0 \\ &\text{Otherwise} \quad WAC_{n,d} = WAC_{n,d} \end{aligned} \qquad (6)$$

Where SWS_{n-1} is the soil water stress index of year *n-1*. $REW_{n,d}$ is the relative soil water content extractable by plants in day *d* of year *n*. $Ta_{n,d}$ is the air temperature in day *d* of year *n*. psink1 and psink2 are parameters. pwood1 to pwood6 are parameters. $WAC1_{n,d}$ is an intermediate value. $WAC_{n,d}$ is the actual wood allocation coefficient simulated in day *d* of year *n*.

The wood growth resumption of *F. sylvatica* is known to occur simultaneously with budburst (Michelot et al., 2012) and we simulated consequently the day of wood growth onset for this species based on the leaf phenology sub-model of CASTANEA. For the other species involved in this study, the day of growth cambial onset was simulated annually using a simple model (N. Delpierre, N.K. Martin-StPaul and A. David, *unpublished results*) that was based on temperature

sums (Guillemot et al., 2015b, Chap. 2). The cessation of the period with possible C allocation to wood growth was based on published results (Bouriaud et al., 2005; Michelot et al., 2012; Lempereur et al., 2015) and fixed to the day 230 and 300 for deciduous and evergreen species, respectively. The phenology of wood growth was simulated in the three versions of the model.

2.1.3 Storage and fine root compartments, interactions with other pools

The storage and fine root compartments competed for C supply: their competition abilities were set according to their C stocks and were ruled by functional equilibria. The allocation to fine roots was based on the hypothesis of a functional homeostasis in water transport within trees (Magnani et al., 2000): the fine root pool was given an annual objective in terms of C stock, which was deduced from the simulated LAImax by using the implementation described in Davi et al., (2009). The competition ability of the fine root pool was modulated as its stock diverged from its annual objective. The competition ability of the storage pool increased when its stock became too low, to avoid a complete C depletion. In case of extremely low C reserve stock during the C demanding leaf formation period, the storage pool interacted with the leaf compartment: daily LAI increase was stopped if the reserve pool dropped below 20gC/m^2. The allocation to reserve and fine roots could occur throughout the year but was strongly constrained by the C allocation to leaf and wood compartments (Fig. 1).

2.2 Field measurements, satellite-derived data and historical climate

2.2.1 Biometric and ecological data

The biometric measurements used in this study were obtained from two complementary sources: the French national forest inventory (NFI, Charru et al., (2010); Vallet & Pérot, (2011)) and a permanent forest plot network (RENECOFOR, Ulrich, (1997)). Because the RENCOFOR network does not include *Q. ilex* plots, it was complemented with measurements from the site of Puéchabon (Rambal et al., 2014).

The NFI sampling was systematic: about one out of ten nodes in a 1 km grid over the national territory was sampled every year. Measurements included the circumference at breast height (CBH), total height and 5 years of radial increment, along with a panel of ecological and

soil characteristics (more details about NFI sampling can be found in Charru et al., (2010) and Vallet & Pérot, (2011)). We used data from the 2005 to 2012 NFI measurement campaigns, available on the NFI website (http://www.ifn.fr). Plots were only measured once during this period. We retained plots with i) high abundance in one of the species considered in this study (>65% of above-ground wood volume) ii) intermediate to mature forest stand (age >30 years old and above-ground wood volume > 60m^3). The final dataset comprised 6204, 2050, 1424 and 228 plots of temperate oak (*Q. petraea* and *Q. robur*), *F. sylvatica*, *P. abies* and *Q. ilex* stands, respectively. The stand basal areas were calculated from the CBH inventories. For each plot, the standing above-ground wood biomass was calculated in the year n (i.e., the year of the sampling) and in the year n-5 (Supplement S1) using biometric measurements and species-specific allometric equations (Rambal et al., 2004; Vallet et al., 2006). The above-ground wood biomass increment (AWBI) between the year n-5 and n was then inferred and divided by 5 to obtain the average annual AWBI. Soil texture estimates were obtained from a soil trench dug at the centre of each IFN plots, and the SWHCs were inferred (Cheaib et al., 2012). The depth of the trench was limited to 70 cm.

The RENECOFOR network included measurements from 26, 16 and 6 plots of temperate oak, *F. sylvatica* and *P. abies* stands, respectively; along with the *Q. ilex* Puéchabon site. Biometric measurements consisted of dendrochronological sampling conducted in 1994 (2008 for the Puéchabon site) and extensive CBH surveys that were combined to calculate past annual AWBIs on each plot. A detailed description of the dataset and of the biomass increment calculation can be found in Guillemot et al., (2015b, Chap. 2). We only retained in the analyses AWBIs of the 1980-1994 period, to reduce the risk of unreported thinning or windthrow events that may have affected the AWBI calculation. The past management of the Puéchabon site being well documented, we kept the original period of 1966-2008 (Guillemot et al., 2015b, Chap. 2). The SWHCs were estimated using texture measured at two soil pits per plot to a depth of 1 m (Brêthes & Ulrich, 1997).

2.2.2 Non-structural carbohydrate data

The measurements of TNC used in this study were obtained from a global meta-analysis (A. Sala & J. Martínez-Vilalta, *unpublished data*) and comprised measurements of stem saplings and mature forest tree sapwood from throughout Europe. The period (season) of data collection was

not homogeneous across the dataset. Data amounted to 76, 48 and 23 records in temperate oak, *F. sylvatica* and *P. abies*, respectively. We complemented this dataset with 9 measurements on *Q. ilex* lignotuber from Galiano et al., (2012) and Rosas et al., (2013).

2.2.3 Satellite-derived data

The normalized difference vegetation index (NDVI) estimates of the MODIS/TERRA surface reflectance product at a 250 m resolution (MOD09GQK, Earth Observing System Data Gateway) were extracted on a daily basis over the 2001-2012 period for each IFN sites. Because the coordinates of the IFN sites have an uncertainty of 500 m, we extracted the NDVI estimates of all the MODIS cells that surrounded the IFN sites. Following the procedure suggested in Hmimina et al., (2013), we retrieved the maximum NDVI value (NDVImax) observed on each MODIS cell by fitting a Gaussian mixture model (GMM, McLachlan & Peel, (2004)) on the raw NDVI data, assuming a quadrimodal distribution. The fitted Gaussian distribution with the highest mean was assumed to describe the fluctuations of annual maximum NDVI over the 2001-2012 period. We retained the 0.95 quantile of this distribution as the observed NDVImax. The NDVImax values of the cell surrounding a given IFN site were then averaged. The IFN sites surrounded by non-forest cells were discarded. NDVImax values were then converted to the maximum fraction of absorbed photosynthetically active radiation (FAPARmax, Fig. 2) and then to LAImax, using the relations provided by Knyazikhin et al., (1999). The relationship between the FAPARmax that was observed at the IFN plots and a panel of biometric and bio-climatic variables were assessed (Supplement S2). In this exploratory step, the FAPARmax was used because satellite-derived products are more reliable for FAPAR than for LAI, mainly because of saturation effects (Seixas et al., 2009; McCallum et al., 2010).

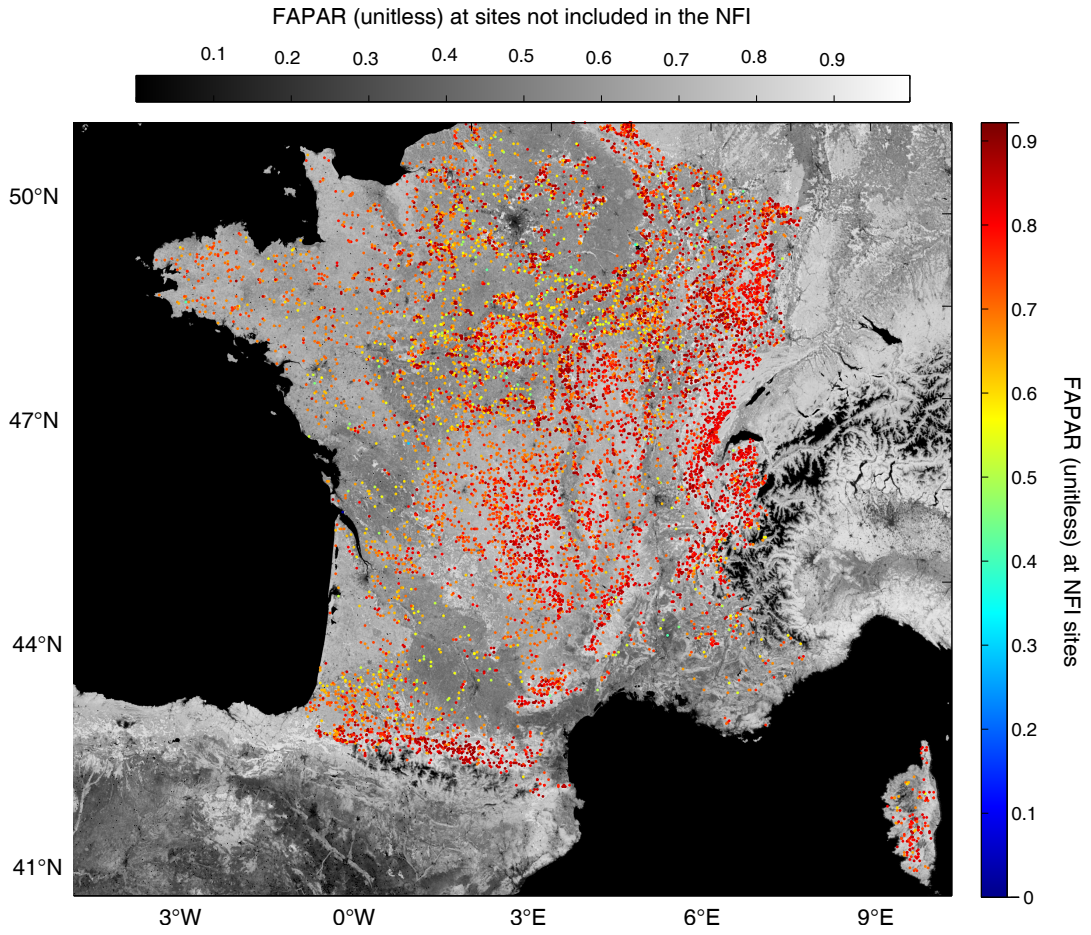

Figure 2: Map of the satellite-derived FAPAR values (MODIS product). The FAPAR values at the IFN sites are indicated in colour.

2.2.4 Historical climate data

The climate dataset that was required to force the CASTANEA model included temperature, precipitation, global radiation, wind speed and air relative humidity on a daily or an hourly basis. For the calibration/evaluation procedure, we relied on the SAFRAN atmospheric reanalysis (Vidal et al., 2010) on the hourly temporal scale and 8km spatial resolution.

2.3 Model calibration and evaluation

We selected half of the NFI AWBI data as calibration dataset, using a random sampling stratified by age, water stress and low temperature stress. The LAImax sub-model was calibrated using the FAPAR-derived LAImax values (Table 1). For each set of parameters that were evaluated during the optimization procedure, the model was run over 30 years by looping 3 times the 2001-2012

period, which corresponds to the observation period of satellite-derived LAImax. The first 20 years of simulations were used as a 'spin-up' period, to ensure that the LAImax simulations were at steady-state. The LAImax values simulated in the last 10 years were then averaged and compared to observations. The resulting calibrated LAImax sub-model was evaluated against the evaluation IFN dataset and used in the subsequent calibration of the wood allocation sub-model.

The calibration of the three versions of the wood allocation sub-model was based on the NFI data. Because there was an important uncertainty associated with the SWHC measurements at the IFN sites, five SWHC values were calculated for each site by adding the following values to the measured SWHC: +20%, +10%, 0, -10%, -20%. For each set of parameters that were evaluated during the optimization procedure, we retained the SWHCs that maximized the observation-simulation agreement. The same SWHC fitting procedure was used for the evaluation of CASTANEA using the IFN wood growth measurements. Only a subset of parameters of Eq. 6 was involved in the calibration of the FULL version (Table 1). The values of the parameters that were not involved in the optimization procedure (pwood3 and pwood5) were based on the results of a previous study (Guillemot et al., 2014, Supplement S3, Chap. 4).

Sub-models	Versions	Description	Related Equations	Parameters to be optimized
LAI				
Simulation of the annual value of LAImax	-	-	Eq. 1	plai1 plai2 plai3
C allocation to wood				
Simulation of the annual woody biomass increment (AWBI)	**CST**	The allocation coefficient to wood is fixed at a constant value every year. No sink control of wood growth. No lagged effect of the previous year's water stress.	*Eq. 2*	pwood1
	STD	The allocation coefficient is related to the age of the stand. There is no sink control of the wood growth. There is no lagged effect of the previous year's water stress on the allocation of C to wood. It is the standard version of CASTANEA.	*Eq. 3*	pwood1 pwood2
	FULL	The Allocation coefficient is related to the age of the stand. There is a sink control of the wood growth. There is a lagged effect of the previous year's water stress on the allocation of C to wood.	*Eq. 4* *Eq. 5* *Eq. 6*	pwood1 pwood2 pwood4 pwood6 psink1 psink2

Table 1: Description of the sub-models of the C allocation scheme involved in the optimization process.

The parameter optimizations of the LAImax and wood allocation sub-models were based on the MCMC Metropolis-Hastings algorithm (Metropolis et al., 1953; Van Oijen et al., 2005). The cost function was defined as the averaged squared data-model mismatch ('least-squares optimization', Richardson et al., (2010)). Prior distributions for each parameter were assumed to be normal with large standard deviations (Supplement S4). For each species and for each sub-model, the parameter space was explored for at least 25,000 iterations. The resulting posterior distributions were constituted by the 1000 parameter sets that best matched to the data. The presented sub-model performances are averages of 2000 runs using the final posterior parameter distribution and tested against the evaluation dataset (Fu et al., 2012). The optimization procedure relied on an *ad hoc* routine coded in R (N. Delpierre, N. K. Martin-StPaul, *unpublished routine*) using the snow package (Tierney et al., 2008).

The evaluation of the model performances included:

- An inter-site evaluation using the NFI AWBI data that were not involved in the calibration process. 'Simulations' and 'observations' refer to averages of AWBI over 5 years in this case.
- An inter-annual evaluation. The calibrated models were confronted to the annual AWBI from the RENECOFOR network. Observations and simulations were preliminarily standardized in order to remove tree-age related growth trend and isolate the inter-annual AWBI variability. The standardization relied on a double detrending process that was based on an initial negative exponential or linear regression, followed by a fitting of a 30-year cubic smoothing spline with 50% frequency response cut-off (Mérian & Lebourgeois, 2011). 'Simulations' and 'observations' refer to annual AWBI in this case.

The performances of the three model versions were assessed using the coefficient of determination (R^2), average bias (AB,Vanclay & Skovsgaard, (1997)), root mean square error (RMSE) and relative root mean square error (RMSE divided by the mean of the observations, rRMSE).

Additionally, the FULL version was evaluated using TNC data. The annual minimum and maximum C storage concentration averaged over 5 years in the NFI evaluation dataset were confronted to the observed TNC. The simulated C reserve concentration was the ratio of the C reserve pool to the sapwood stock. The simulations were converted in mgC/g of dry matter,

assuming 50% of C content in dry matter.

2.4 Projections of wood growth in European forests

Projections of the future European climate on the daily temporal scale and 0.5° spatial resolution were obtained from the SMHI RCA4 regional climate model (RCM, Samuelsson et al., (2011)), driven by boundary conditions from the MPI earth system model (a global circulation model, GCM, Bathiany et al., (2010)). A preliminary study revealed that the MPI-ESM/RCA4 projections was representative of the projections obtained from five GCM/RCM combinations currently involved in the CMIP5 project over Europe (Supplement S5). We accounted for the uncertainty associated with the future anthropogenic C emissions by considering three contrasted climate change scenarios (RCP 2.6, RCP 4.5 and RCP 8.5, Moss et al., 2010). The 21st century was divided in three 25-years periods (P0: 2006-2030, P1:2040-2064, P2: 2075-2099). For each period and each RCP scenario, climate projections data were bias-corrected to ensure statistical agreement with the observation-based WATCH forcing data (Weedon et al., 2011) over the period 1984 2008. The bias correction was based on quantile mapping, i.e., we corrected the frequency distribution of the individual climatic events for each variables (Ruffault et al., 2014), using the qmap R package (Gudmundsson, 2012). The SWHCs used by CASTANEA were derived from the European Soil Database; available at the European Soil Data Centre (http://eusoils.jrc.ec.europa.eu, Panagos et al., (2012)). We accounted for the uncertainty regarding the long-term effect of elevated [CO_2] on plant physiology by considering two contrasted assumptions about the persistence of [CO_2] effect on photosynthesis (Cheaib et al., 2012; Reyer et al., 2014). Under the assumption of no fertilization effect of [CO_2] on plant, the [CO_2] value forced in the model was kept to the value of 380 ppm (observed value at the beginning of period P0) for each period and RCP scenario (Table 2). When a fertilization effect was assumed, [CO_2] was fixed at the value expected under the different RCP scenarios and periods (Table 2). No progressive acclimation effect was accounted for.

	Fert. Effect			*No Fert. Effect*
Scenario	**RCP2.6**	**RCP4.5**	**RCP8.5**	
Period				
P0	400	400	400	380
P1	440	480	570	380
P2	410	520	830	380

Table 2: $[CO_2]$ values prescribed for the wood growth projections. The $[CO_2]$ values are function of the C emission scenarios (RCP2.6, 4.5, 85), the time period (P0, P1, P2) and the assumption made on the fertilization effect (Fert. Effect) of the elevated $[CO_2]$ on plant functioning.

We aimed at evaluating the implications of the sink limitations of growth for the projected European forest productivity. The new version of the CASTANEA model (FULL) and the standard version (STD) were run for each period and species under the different assumptions described above, regarding climate and plant physiology (total of 144 runs Fig. 3). We combined the simulated species-specific AWBIs values by retaining for each grid cell the maximum value among the four studied species, in order to obtain 36 synthetic maps of possible wood growth evolution (Fig. 3).

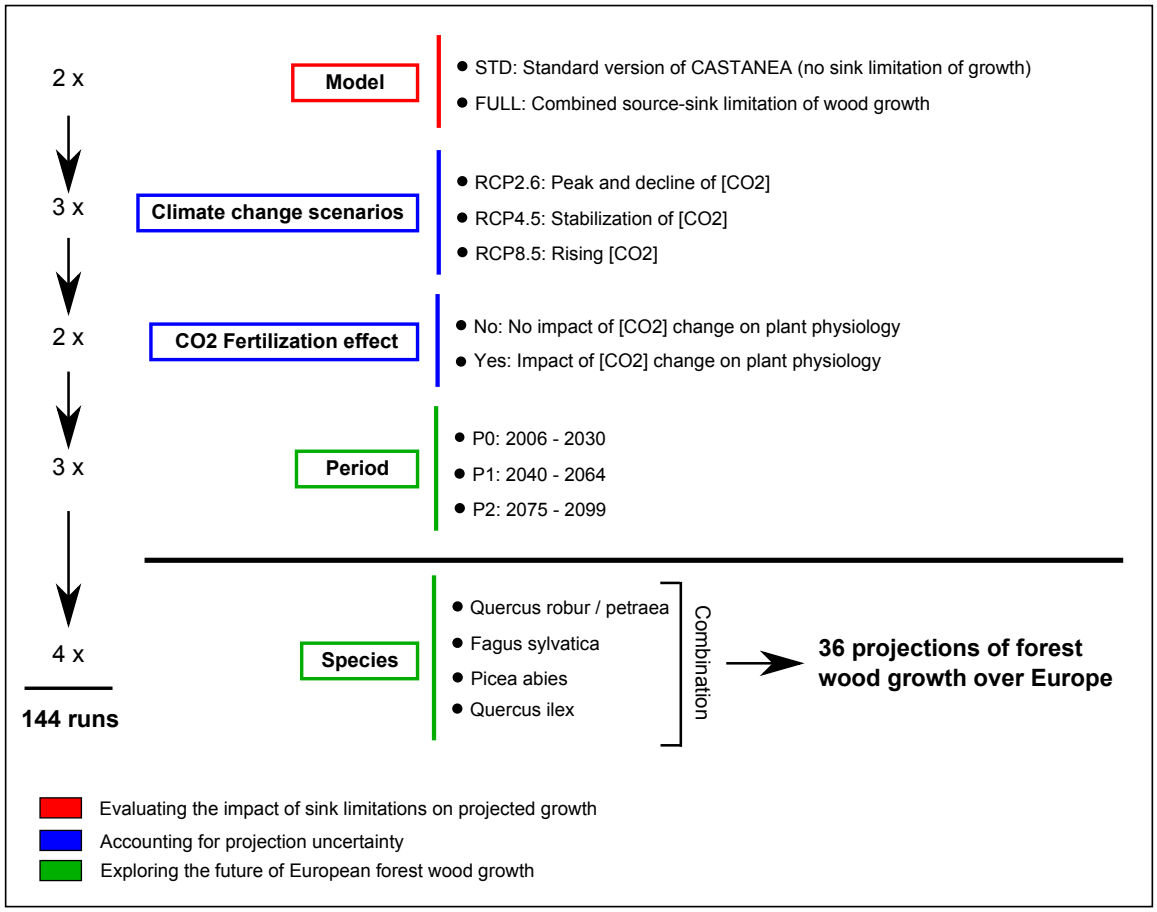

Figure 3: Schematic diagram of the wood growth projection experiments.

To evaluate the evolution of wood growth simulations from current to future climate we computed the AWBI anomalies in period P1 and P2 compare to the reference period P0:

$$A_{VXPY} = \frac{\overline{AWBI_{VXP0}} - \overline{AWBI_{VXPY}}}{\overline{AWBI_{VXP0}}} \times 100$$

where A_{VXPY} is the anomaly simulated by the model version VX in period PY on the considered grid cell, $\overline{AWBI_{VXP0}}$ and $\overline{AWBI_{VXPY}}$ are the average AWBI simulated on the considered grid cell over the period P0 and PY, respectively (X=STD or FULL; Y=1 or 2). The simulated anomalies were analysed at the European and sub-European scale by defining four contrasted climatic sub-regions, based on the work of (Metzger et al., 2005): Atlantic, Continental, Boreal/Alpine and Mediterranean. The relative importance of climate, $[CO_2]$ fertilization effect and sink limitations in explaining anomaly variations over Europe were evaluated in period P1 and P2 using a non-parametric analysis of variance that was based on permutation tests (PERMANOVA, Anderson, (2001)). Non-parametric analysis was required as data were not normally distributed. PERMANOVA was conducted using the vegan R package (Oksanen et al., 2007).

3 Results

3.1 Performances of the carbon allocation modelling

3.1.1 LAImax

The satellite-derived FAPARmax retrieved on IFN plots was significantly linked to an aridity index (P-ETP summed from April to August, Fig 4) in *F. sylvatica*, *Q. petraea/ robur* and *P. abies*. Among these three species, the reported decline in FAPARmax at dry sites was more pronounced in *Q. petraea* and minimum in *P. abies*. Aridity explained a moderate part of the overall FAPARmax variability (R^2<15), however no other explanatory variables, including biometric and site fertility data, were found to be linked to the FAPARmax of these three species. No significant dependences were highlighted in *Q. ilex*.

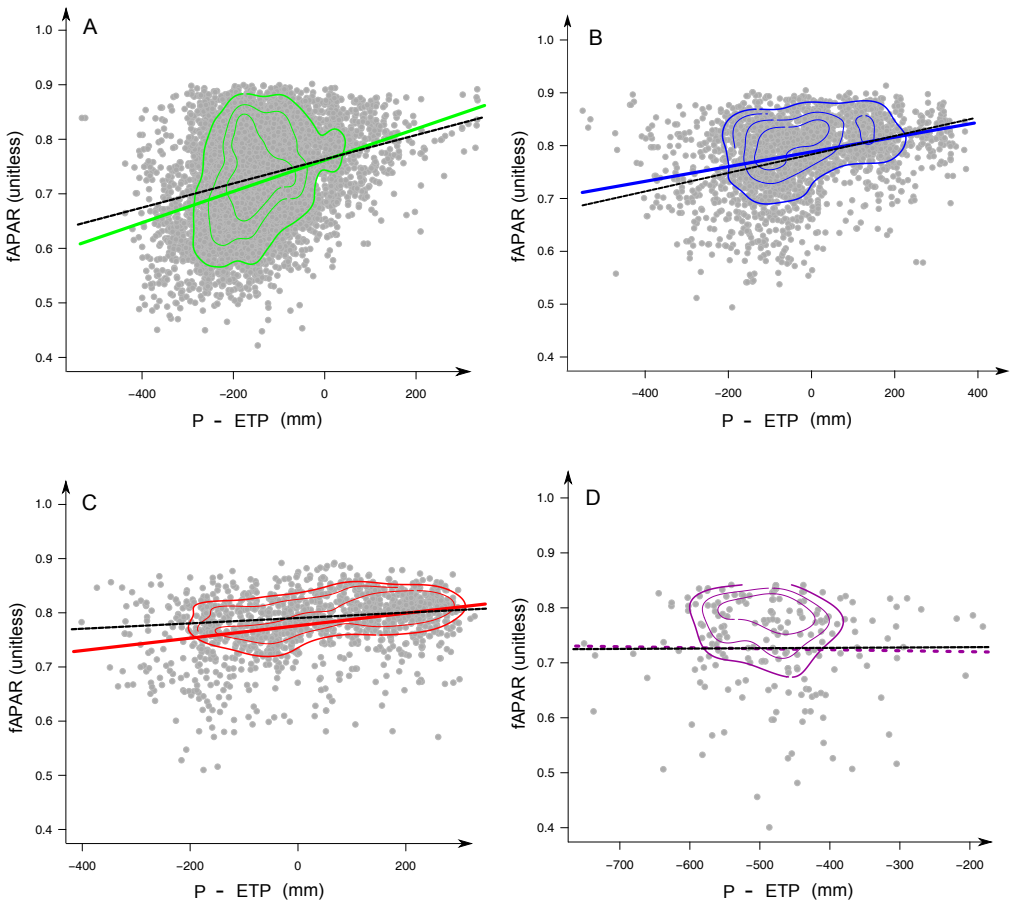

Figure 4: Relationship between the FAPAR values (observed and simulated) and the aridity simulated at the IFN sites. A: *Quercus robur/petraea*, B: *F. Sylvatica*, C: *P. abies* and D: *Q. ilex*. Solid, coloured lines are the observed FAPAR vs aridity regression lines. Dotted, black lines are the simulated FAPAR vs aridity regression lines.

The FAPARmax simulated at the IFN sites comprised in the evaluation dataset showed a decline with aridity that was consistent with the aridity-related decline of the satellite-derived FAPARmax observations (Fig. 4) that we observed in *F. sylvatica*, *Q. petraea/ robur* and *P. abies*. Because we found no significant dependences of FAPARmax to the aridity index for *Q. ilex*, the drought-induced adjustment for this species was based on the model suggested in Ogaya & Peñuelas (2007).

Submodel	Species	Parameters					
		plai1	**plai2**	**plai3**			
LAI	*Q. petraea/robur*	5.22	1.52	0.058			
	F. sylvatica	5.31	2.66	0.059			
	P. abies	6.26	2.03	0.081			
		pwood1	**pwood2**	**pwood4**	**pwood6**	**psink1**	**psink2**
Wood growth	*Q. petraea/robur*	0.54	-0.0015	-0.11	50.7	0.31	5.5
	F. sylvatica	0.62	-0.0013	-0.11	50.9	0.28	5.6
	P. abies	0.69	-0.0024	-0.12	50.4	0.26	6.2
	Q. ilex	0.55	-0.0025	-0.12	52.9	0.28	6.1

Table 3: Values of the optimized parameters. Units: plai (m^2 leaf/m^2 soil); plai2 (m^2 leaf/m^2 soil); plai3 (m^2 leaf/m^2 soil); pwood1 (unitless); pwood2 ($year^{-1}$); pwood4 (unitless); pwood6 (unitless); psink1 (unitless); psink2 ($°C$).

3.1.2 Wood growth

The FULL version of CASTANEA performed satisfactorily in predicting the wood growth at the IFN sites retained in the evaluation dataset (Fig. 5). CASTANEA was able to capture the changes in 5-year AWBIs across a large number of sites (n=3102, 1025, 712, 114 in *Q. petraea/robur*, *F. sylvatica*, *P. abies* and *Q. ilex*, respectively) in the four species studied. Interestingly, the CASTANEA performances were good in all the age classes of the IFN chronosequence (Fig. 6). In particular, the observed age-related decline in AWBIs was well predicted by the model, accordingly to the age-related decline in the allocation to wood that was formalized in Eq. 4. The model was also able to satisfactorily predict the inter-annual variability of AWBIs in 763 site-years (Fig. 7). We observed that the representation of sink limitations in CASTANEA increased substantially its ability to simulate the spatial and temporal variations in AWBIs (Fig. 8). The data-model agreements reported for the three CASTANEA versions calibrated independently (FULL, STD and CST) were indeed always higher in the FULL model version.

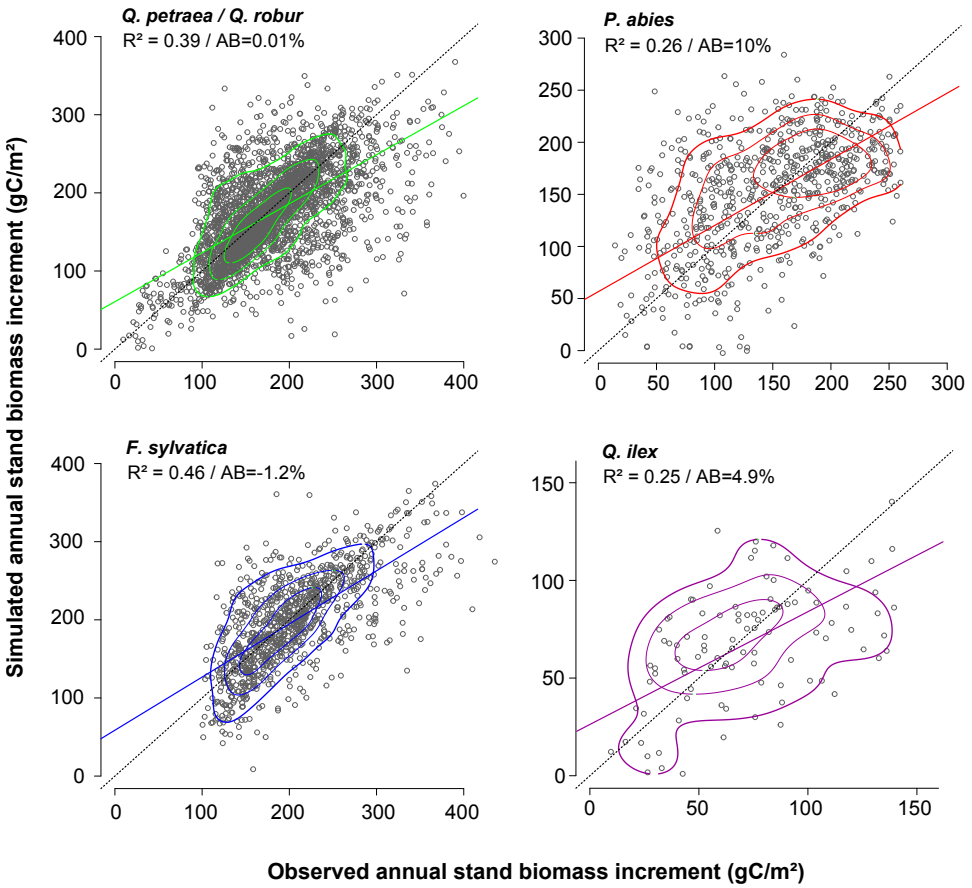

Figure 5: Spatial evaluation of the CASTANEA model using the IFN wood growth dataset. Each dot corresponds to the 5-year AWBI measured at an IFN site. Coloured lines are observation vs simulation regression lines. Black lines are 1:1 lines.

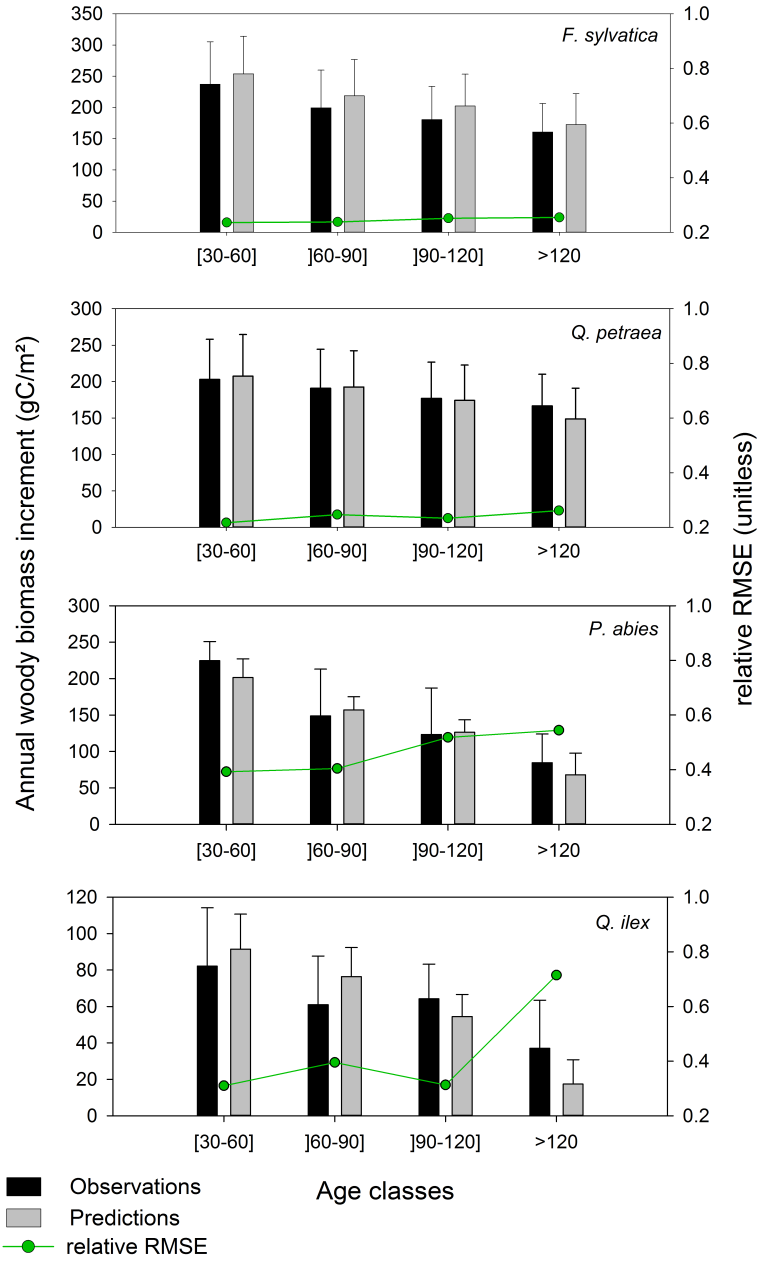

Figure 6: Evaluation of the CASTANEA model by age classes using the IFN wood growth dataset.

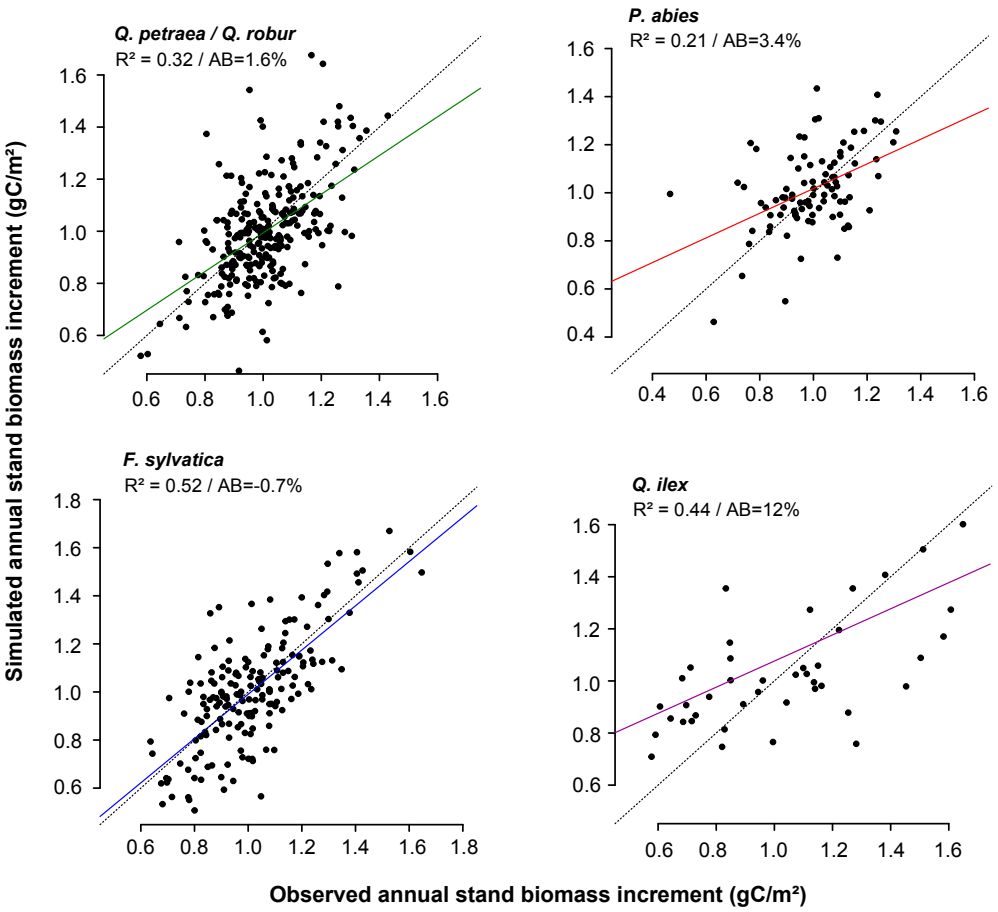

Figure 7: Temporal evaluation of the CASTANEA model using the RENECOFOR wood growth dataset. Each dot corresponds to a site-year measurement of AWBI. Coloured lines are observation vs simulation regression lines. Black lines are 1:1 lines.

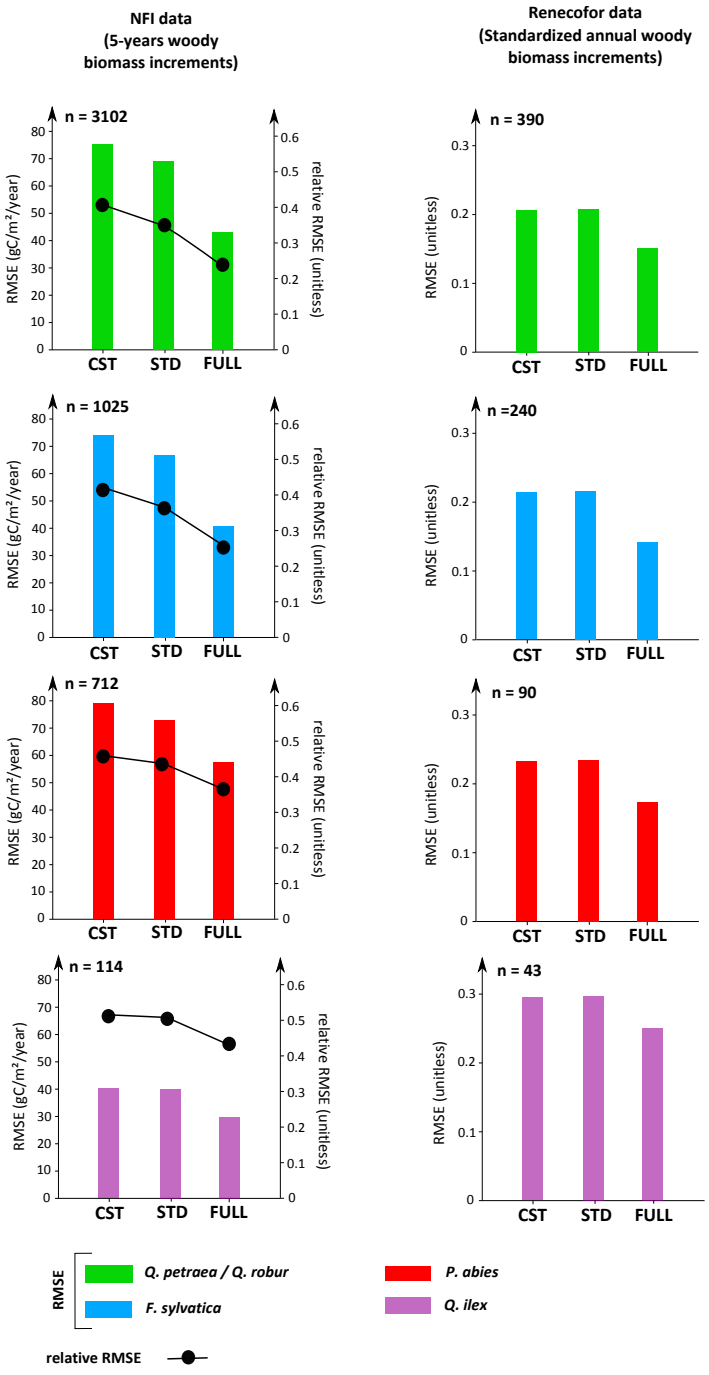

Figure 8: Comparison of the performances of the CST, STD and FULL versions of CASTANEA using wood growth measurement datasets.

3.1.3 Storage

The fluctuations of the C reserve pool simulated by CASTANEA appeared to be realistic (Fig. 9): the annual maximum and minimum C reserve pool simulated at the IFN plots were generally in the range of species-specific observations sampled across a large panel of environmental conditions over Europe.

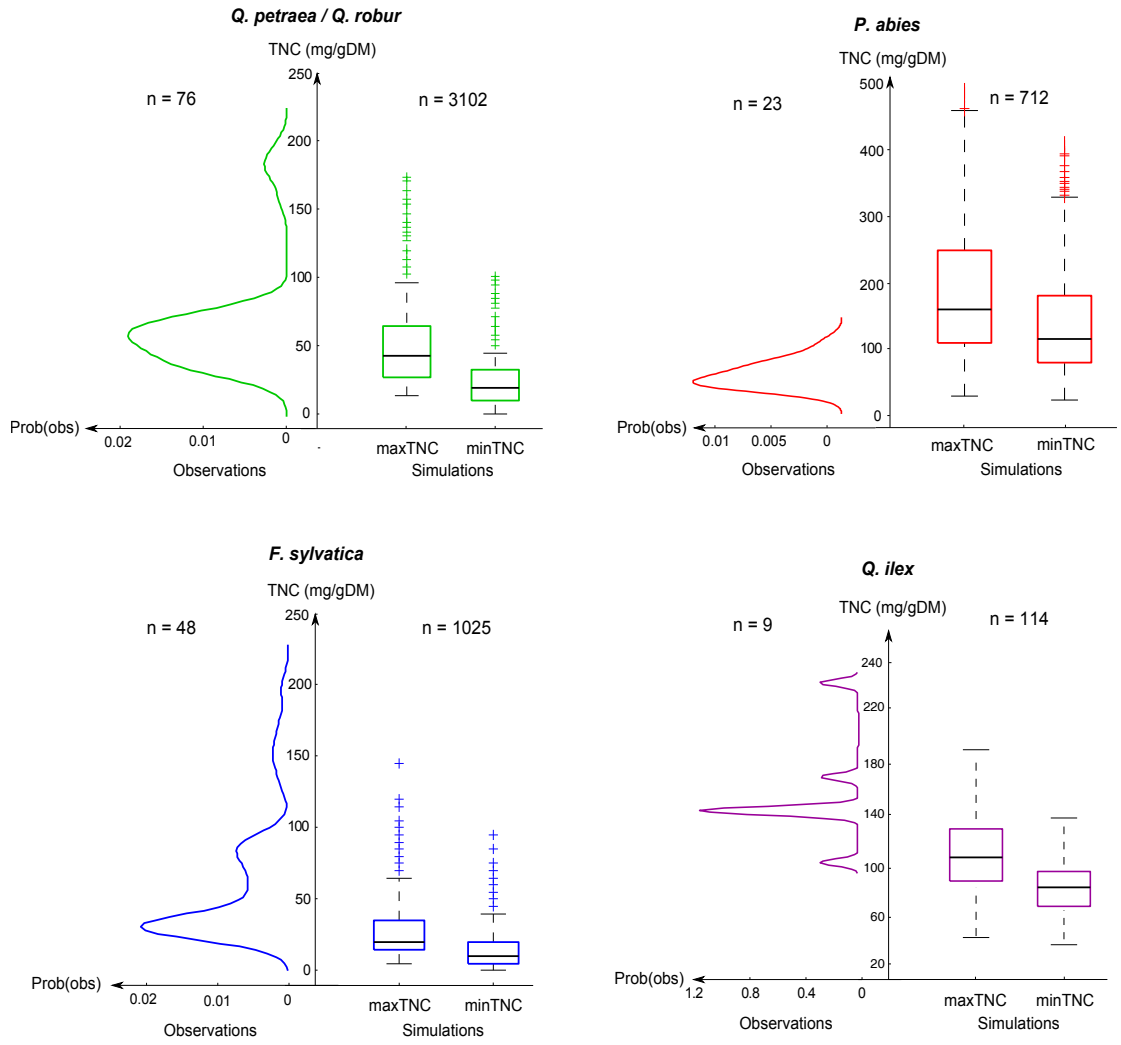

Figure 9: Comparison of the C reserve that was simulated by CASTANEA (FULL version) at the IFN sites with C measurement of reserve from a European dataset.

3.2 Implications of sink limitations for wood growth projections

The maps of the simulated AWBI anomalies revealed that the FULL and STD versions of CASTANEA both predicted an increase of forest wood growth in the northern part of Europe and a decline in its southern part (Fig. 10). The relative importance of these two trends appears to be strongly determined by the assumption made about the $[CO_2]$ fertilization effect: when assuming a persistent $[CO_2]$ fertilization effect, a large part of Europe is expected to experience an increase in wood productivity, even under high C emission scenario (RCP8.5, Fig. 10, bottom plots, results for other scenarios are provided in Supplement S6). The two model versions however differed substantially in their predictions of the spatial pattern of future wood growth changes. The predictions of the FULL version were more spatially contrasted,

with more pronounced decline in continental Europe and higher increase in northern Europe. More generally, the predictions of the FULL version seem to be more affected by regional and sub-regional environmental gradients.

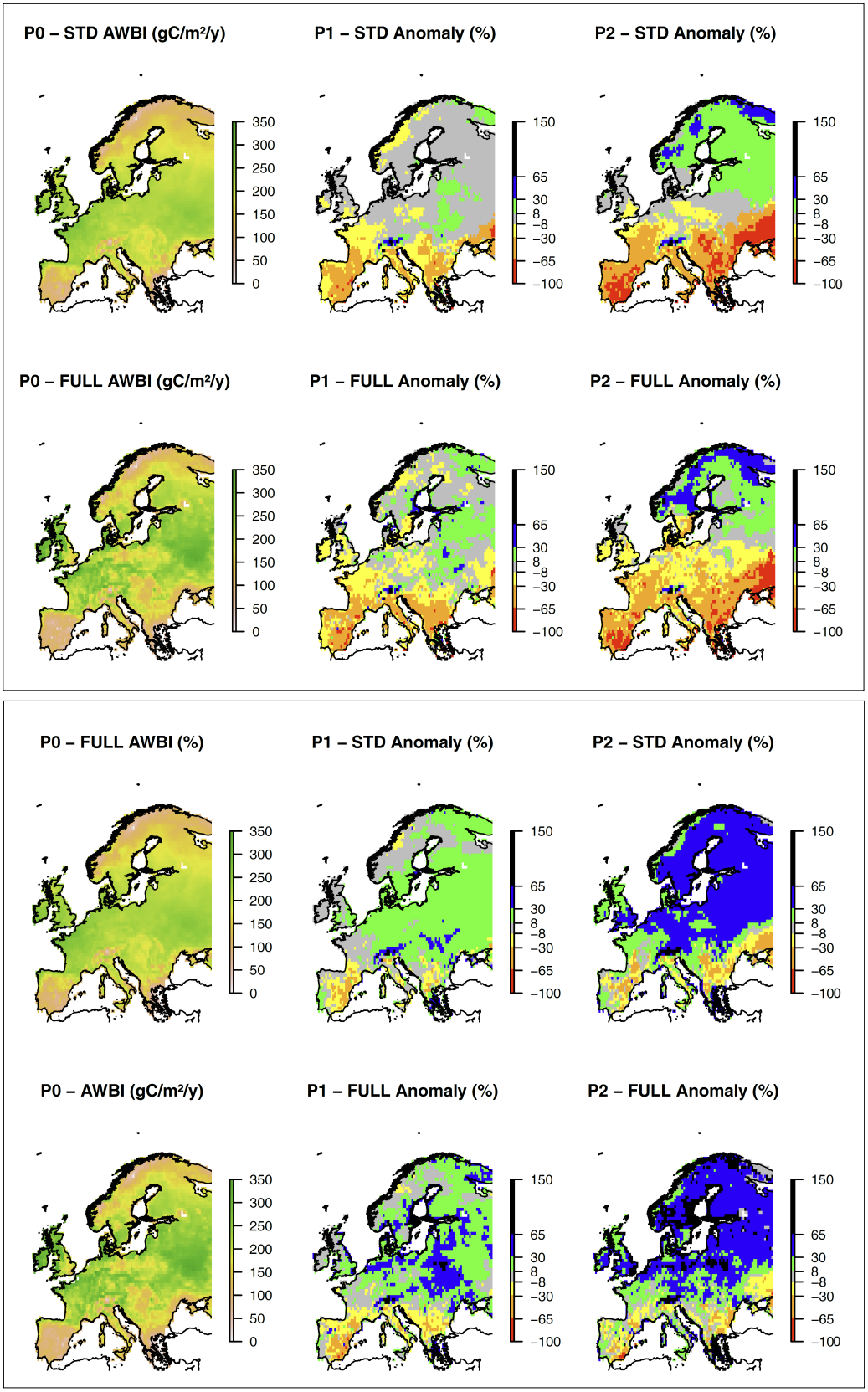

Figure 10: Map of the projections of the wood growth in European forest under the RCP 8.5 C emission scenario. The simulation from the STD and the FULL version of CASTANEA are compared under the assumption of no $[CO_2]$ fertilization effect (top panel) and persistent $[CO_2]$ fertilization effect (bottom panel).

These statements are confirmed when comparing the two model versions on the sub-regional scale (Fig. 11).The assumption about [CO_2] fertilization effect changed the average anomaly from positive to negative in most of the European area (Atlantic, Continental and Mediterranean sub-regions, Fig. 11, top subplots). Boreal / Alpine sub-region was nonetheless expected to experience an increase in wood productivity regardless of the [CO_2] fertilization assumption. The representation of the sink limitations did not change these trends and they only marginally affected the average anomalies in most of the regions. However, the absolute differences between the predicted anomalies revealed that the FULL and the STD CASTANEA versions actually differed substantially in all regions (Fig. 11, bottom subplots). The predictions of the FULL version were therefore more spatially heterogeneous, i.e. higher than the predictions of the STD version in areas of favourable growth conditions, and lesser otherwise. These differences are dampened when aggregated at the regional and European scales.

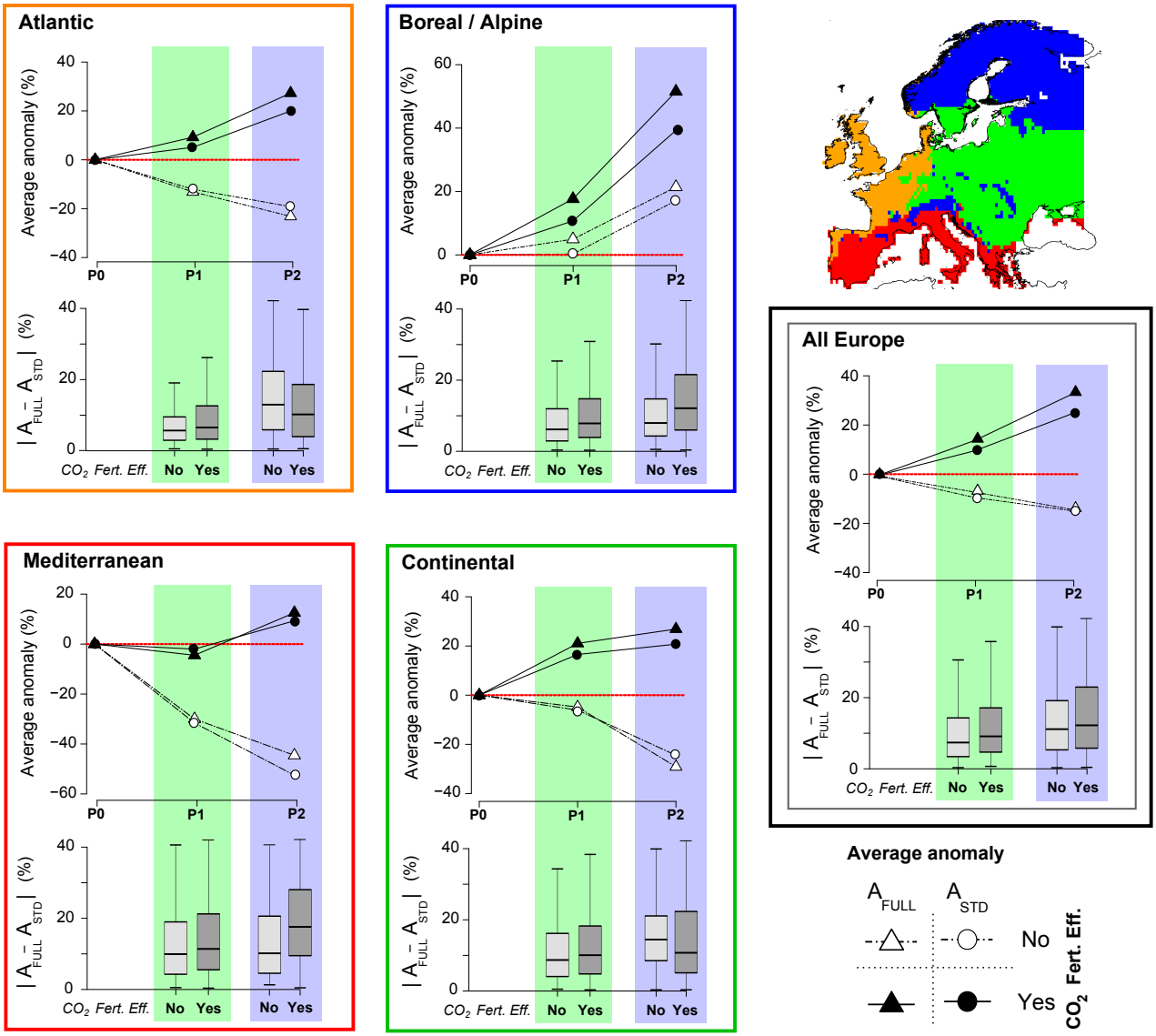

Figure 11: Projections of the average growth anomalies (top plots) and absolute differences between the predictions of the STD (A_{STD}) and the FULL (A_{FULL}) version (bottom plots) under the RCP 8.5 C emission scenario. CO_2 Fert. eff. is the assumption made regarding the fertilization effect of elevated [CO_2] on plant: Yes corresponds to a persistent effect, No corresponds to no fertilization effect.

In line with this statement, the average spearman correlation coefficient between growth anomalies and soil water stress index for the RCP8.5 scenarios (across all sub-regions, periods and [CO_2] fertilization assumption) was significantly higher with the FULL version predictions (Fig. 12).

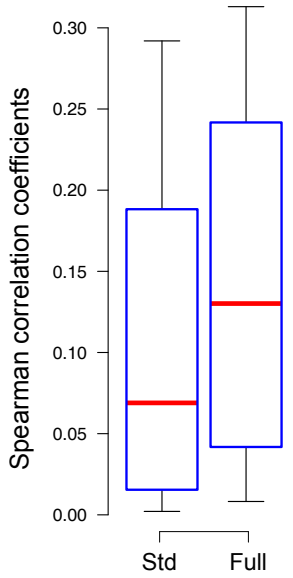

Figure 12: Correlation between the SWS index and the growth anomalies. The Spearman correlations have been evaluated for each sub-region and each time periods (P1 and P2). The values of the correlation coefficients that were obtained with the STD and the FULL model version are compared.

The PERMANOVA analysis indicated that, for the period P1 (2040-2064), the changes in AWBI anomalies explained by the implementation of sink limitation were comparable (36%) to the changes induced by climate scenario variability and by the different assumptions about CO_2 fertilization effect on plants (Fig. 13). The relative importance of the representation of the sink limitations then decreased in period P2 (16%), climate scenarios and CO_2 fertilization assumptions both being similarly important factors explaining the changes in simulated anomalies.

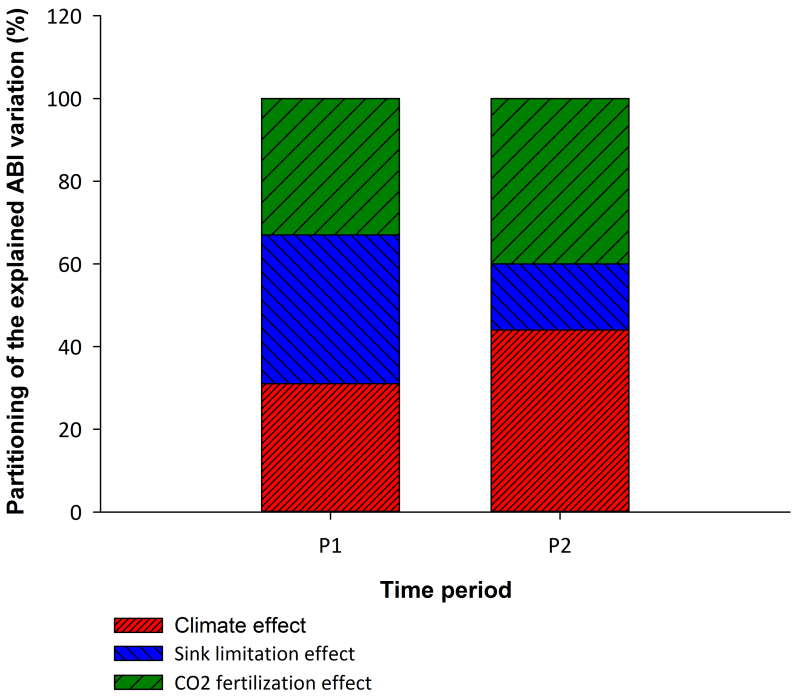

Figure 13: Analysis of the variance of the growth anomalies (obtained using the PERMANOVA procedure) during the period P1 (2040-2064) and the period P2 (2075-2099).

4 Discussion

4.1 Simulating the annual allocation of C in trees

For three decades, TBMs have been used to understand and anticipate the terrestrial biogeochemical cycling and forest functioning on scales that ranged from local to global (Running et al., 1987; Aber & Federer, 1992; Mäkelä et al., 2000). Stimulated by the increasing number of eddy-covariance flux measurements sites (Baldocchi, 2008), substantial progress have been made in the modelling of the water and C gas exchanges between the forests and atmosphere. Consequently, the simulation of gas exchanges have thus far been at the centre of the projections of the effects of climate change on forests (Morales et al., 2007; Reyer et al., 2014). However, the partitioning of the sequestered C among the tree compartments (i.e., the within-tree C cycling) recently turned out to be a major, overlooked source of uncertainty in TBMs projections (Carvalhais et al., 2014; Friend et al., 2014). Problematically, the TBMs used on regional to global scales do not performed well at predicting within-tree C allocation (De Kauwe et al., 2014; Friedlingstein et al., 2014). Here, we addressed this limitation by implementing in the

CASTANEA TBM a new C allocation scheme, which incorporated some of the most recent hypotheses regarding the environmental and internal drivers of the within-tree C cycling. CASTANEA was successfully evaluated at almost 5.10^3 sites from throughout France, for four species that represent the main European biomes: temperate deciduous broadleaf forests (*F. sylvatica*, *Q. petraea/robur*); high-latitude and high-altitude evergreen needleleaf forests (*P. abies*) and Mediterranean forests (*Q. ilex*).

4.1.1 LAI

The negative effect of water stress on FAPARmax values observed at the IFN sites was consistent with the ecohydrological equilibrium hypothesis (Eagleson, 1982). This hypothesis states that the ecosystems develop a vegetation density that maximize C sequestration and minimize water loss. The canopy density is therefore expected to decline with aridity because the development of the plant canopy increases the quantity of water that is lost by evapotranspiration. We observed a significant adjustment of FAPARmax to water stress in species from temperate (*F. sylvatica*, *Q. petraea/robur*) and high-latitude and high-altitude forests (*P. abies*), i.e. at sites that were not expected to be strongly water-limited. This finding agrees with recent studies (Choat et al., 2012; Lévesque et al., 2014), which indicate that there is a global (i.e. xeric and mesic forest types) convergence in the sensitivity of forest to drought. Although the adjustment of standing biomass and LAImax to water stress received ample evidence in Mediterranean oak forests (Joffre & Rambal, 1993; Limousin et al., 2009; Barbeta et al., 2014), we did not find a significant correlation between the FAPARmax and water stress in *Q. ilex*. This absence of correlation may have resulted from our plot selection, in which i) we retained a small number of sites (114 sites in the IFN evaluation dataset) with medium to high stand biomass density, and ii) we retained plots from southern France, i.e., a small portion of the total Mediterranean area (Metzger et al., 2005). Our dataset may therefore not have encompassed the large water stress gradients that possibly induce significant LAImax changes (Ruffault et al., 2013). Alternatively, this result may be attributed to the limitations of our modelling approach: the resolutions of the SWHC and climate used in this study may be too coarse to accurately simulate water balance in the Mediterranean area, which is strongly heterogeneous at fine scale (<1 km^2) in terms of climate and soil (Ruffault et al., 2013). The ecohydrological equilibrium of LAImax has long been implemented in models by assuming optimal water use efficiency in plants (Nemani & Running,

1989; Kergoat, 1998; Mouillot et al., 2001). Interestingly, CASTANEA was able to predict the decline of canopy density at dry sites (Fig. 4) by simulating the inter-annual fluctuation of LAImax that is induced by water stress (Eq. 1, Bréda & Granier, 1996; LeDantec et al., 2000; Chakroun et al., 2014), without any optimality assumption. Consequently, our modelling of the temporal changes in LAImax accounted for both short (annual) and long (multi-decadal) terms adjustment of LAImax to drought, which has been reported as an important acclimation to water deficit in forests (Maseda & Fernández, 2006; Martin-StPaul et al., 2013) and will affect TBM projections of future forest functioning.

4.1.2 Storage

We used a database of C reserve measurements, which contained observations from throughout Europe, to provide species-specific benchmarks for the predictions of CASTANEA. The CASTANEA predictions of the C stored in the reserve pool were in partial agreement with this database (Fig. 9): in a majority of the IFN sites, CASTANEA predicted annual maximum and minimum C storage content that were in the range of the observed storage content. Although it is an encouraging result toward the complete evaluation of the C allocation scheme, some important questions regarding the CASTANEA performances remained unanswered in this study. Specifically, the active C storage after extreme drought years (Wiley et al., 2013) that was formalized in Eq. 5 is yet to be evaluated using TNC data. The role of the C reserve in the metabolism of trees and its influence on wood growth are indeed important topics (Richardson et al., 2013; Rocha, 2013; Dietze et al., 2014) that may contribute to the understanding of the current forest diebacks observed worldwide (McDowell, 2011) . The testing of hypotheses regarding the effect of the reserve dynamic on growth could only be conducted on the few sites that have been monitored for the extensive survey of the C compartments. This goal is beyond the scope of the modelling approach that we present in this paper.

4.1.3 Wood growth

Ultimately, the fraction of C that is sequestered in tree woody biomass determines an important part of the terrestrial C sink (Pan et al., 2011). The evaluation of the wood growth simulated by TBMs have thus far relied on: i) *biometric tree measurements* (Zaehle et al., 2006; Bellassen et

al., 2011a), which are obtained from forest inventories. The variables used in TBM evaluations include above-ground woody biomass and tree height. ii) *allometric scaling metrics* (Wolf et al., 2011a, 2011b; Smith et al., 2014), such as the ratio between woody and leafy biomass. These allometric relationships are obtained from global biomass datasets (Cannell, 1984; Luyssaert et al., 2007). They are assumed to be driven by universal, biophysical and evolutionary forces and they are therefore used to evaluate the prediction of a given tree compartment stock by relating it to the stocks predicted for the other compartments. iii) *yield tables* (Zaehle et al., 2006; Bohn et al., 2014), which correspond to statistical models calibrated on the regional scale. The yield tables predict the stand wood growth as a function of age and site fertility. All these data sources are used to evaluate the ability of TBMs to predict the typical long term evolution of tree wood stocks. This is much needed and provides important benchmarks for the modelling of the terrestrial C cycling. However, wood stock data are not always suitable to study the processes that underlie C allocation in trees, mostly because they are affected primarily by the age of the considered stand and only secondarily if they do by local environment, which has important effects on C allocation to wood (Campioli et al., 2013; Rammig et al., 2014). Indeed, wood stock is generally poorly related to the partitioning of the C that is sequestered in the ecosystems (Litton et al., 2007). Consequently, TBMs that are currently used on the regional to global scales generally do not perform well at predicting C allocation to wood (Bellassen et al., 2011b; De Kauwe et al., 2014). The C allocation scheme that we present in this study is a first attempt to circumvent this limitation. Although it was based on a straightforward, easily transferable modelling framework (Guillemot et al., 2015b, Chap. 2), it successfully captured the changes in the annual C allocation to wood across 5.10^3 sites (Fig. 5). CASTANEA successfully predicted some important features of the long-term evolution of forest functioning, such as the amplitude of the age-related decline in wood productivity (Fig. 6, Ryan et al., 2006; Zaehle et al., 2006). This result is mostly the consequence of both the simulated decline of the C fraction allocated to wood in old forests and the age-related decrease in the simulated NPP as a result of the increase of the maintenance biomass respiration. CASTANEA also performed well in predicting the inter-annual fluctuations of the C allocation to wood (Fig. 7), which is a current challenge for TBMs (Rocha, 2013). We observed that the combined representation of i) the environmental control of sink activity and ii) the lagged effect of previous year's water stress on wood growth improved substantially the performances of CASTANEA in both the inter-site and inter-annual evaluations (fig. 8). These results are consistent with recent studies (reviewed in Fatichi et al.,

(2014)) reporting that cambial activity is more sensitive than C assimilation to water deficit (Muller et al., 2011; Tardieu et al., 2011) and low temperatures (Körner, 2008; Leuzinger et al., 2013). The lagged effect of previous year's water stress implemented in CASTANEA was a proxy for an active storage of C at the expense of wood growth, following years of low C sequestration (Rocha et al., 2006; Richardson et al., 2013). In a recent report, Guillemot et al., (2015b, Chap. 2) found that the dynamic of the annual C allocation to wood of the four species studied in this paper was subject to complex control processes that included both source (C assimilation) and sink limitations. However, numerous key environmental factors (e.g., nutrients, temperature and water) affect both source and sink activity and there is therefore a risk of 'getting the right answers for the wrong reason' (Fatichi et al., 2014) when using the current generation of TBMs for predicting wood growth in forests. Despite the important correlation among the factors underlying the C source and the sink activity, we found that the representation of the internal and environmental factors affecting directly the cambial activity was needed to predict wood growth using TBMs. Our results indicate that we need to calibrate and evaluate TBMs using annual growth measurement data (i.e., C fluxes) additionally to stand biomass measurement data (i.e., C stocks) to gain more insights into the processes that drive the C allocation to wood. More generally, it is worth considering that over the course of a year, the tree primary meristems produce an amount of leaf, fine roots and fruit biomass that is of the same order of magnitude that the growth of woody biomass (Granier et al., 2008; Campioli et al., 2011; Rambal et al., 2014). Although this is of limited importance when considering tree compartment stocks over the long-term (because wood account for most of the biomass stock), it means that we cannot properly constrain the allocation scheme in TBMs without gaining knowledge on the seasonal and annual growth dynamics of all the tree compartments.

4.2 Projections of the future changes in wood growth over Europe

The projections of the future changes in forest productivity over Europe has been the focus of a number of studies (Morales et al., 2007; Pussinen et al., 2009; Wamelink et al., 2009; Friend, 2010; Reyer et al., 2014). A major originality of our approach is to explicitly project the future changes in wood growth, rather than the future changes in the NPP of European forests. The NPP corresponds to the net amount of C sequestered in trees over a given time period and the wood growth is the fraction of this NPP allocated to wood. The direct environmental limitations

of the sink activity that we discussed above have the potential to decouple the NPP from the wood growth over long time periods (Fatichi et al., 2014), with important implications for the terrestrial C sink. More generally, a whole allocation perspective is needed to correctly interpret the relationship between the changes in forest wood growth and NPP (Doughty et al., 2014). In the following, we discuss the predictions of the STD (source control on wood growth) and FULL (combined source and sink controls on wood growth) versions of the CASTANEA model, with a particular focus on the implications of the sink limitations for the projections of the changes in wood growth.

We found that under the future climate predicted by the MPI-ESM/RCA4 combination and the RCP 8.5 C emission scenarios, the European area was expected to experience important changes in forest wood growth (Fig. 10). Similarly to previous study (Friend, 2010; Keenan et al., 2011; Kirschbaum et al., 2012; Reyer et al., 2014), we observed that the projected trends in growth anomaly for each sub-region was primarily determined by the assumption made about the effect of elevated [CO_2] on plant functioning (Fig. 11). Additionally to its positive effect on C assimilation (Farquhar et al., 1980), the effects of the elevation of [CO_2] that are simulated in CASTANEA include an increase in the water use efficiency (WUE, the ratio of assimilation to transpiration). The empirical stomatal model implemented in CASTANEA indeed stipulates that, for a given relative humidity, the WUE will increase proportionally to [CO_2] (Ball et al., 1987). This hypothesis has recently been supported by data from FACE experiments (De Kauwe et al., 2013). The increase of WUE may therefore at least partly counteract the increase of water deficit expected under climate change (De Kauwe et al., 2013; Keenan et al., 2013). However, enhanced WUE did not always translate into increases in growth, possibly because enhanced drought or nutrient limitations can override the potential benefits of elevated [CO_2] for forest productivity (Peñuelas et al., 2011; Battipaglia et al., 2013; Gómez-Guerrero et al., 2013; Lévesque et al., 2014). Moreover, little is known about the long-term acclimation of photosynthesis to elevated [CO_2] (Leakey et al., 2009). These uncertainties were considered explicitly through two contrasted assumptions about the long-term [CO_2] fertilization effect in order to provide benchmarks for our projections of future growth changes. In the Continental, Mediterranean and Atlantic sub-regions, the sign of the projected changes in wood growth was determined by the assumption made about [CO_2] fertilization effect (positive when assuming a persistent [CO_2] fertilization effect, negative otherwise). The same pattern was observed when

considering the growth anomaly computed at the scale of Europe. This emphasises the necessity of further research on the long term effect of elevated [CO_2] on plants to accurately project the future European C sink. By contrast, the Boreal / Alpine sub-region experienced increases in wood growth regardless of the assumption made about [CO_2] fertilization effect. These qualitative results are consistent with the predictions of previous modelling studies (Morales et al., 2007; Reyer et al., 2014). Moreover, most of the experimental studies that evaluated the past growth trend of European forests report increases in productivity in boreal forests and recent growth declines in the Mediterranean and Continental areas (Boisvenue & Running, 2006; Charru et al., 2010; Kint et al., 2012; Lindner et al., 2014). These results reflect the negative effect of the increasing aridity in southern and central Europe (Dai, 2013) and the benefit of the temperature increases for the functioning of Alpine and Boreal forests (Euskirchen et al., 2006). We projected these trends to continue over the 21st century, although the uncertainty about the [CO_2] fertilization effect on plants precludes any definitive predictions, especially in the mid-latitude European area. The comparison of the magnitude of the growth changes that we projected with previous studies is made difficult by the differences in the GCM/RCM combinations, C emission scenarios, and simulation experiments that have been used. When compared to the most recent attempt to project European forest productivity for the end of the 21st century (Lindner et al., 2014; Reyer et al., 2014), our result showed consistent average values of productivity changes in the Atlantic (+20%), Continental (+20%) and Mediterranean (+10%) sub-regions, under the assumption of a persistent [CO_2] fertilization effect. However, we predicted greater increases of the forest productivity in the Boreal/alpine zone (with values ranging from +20 to +50%) and we generally obtained greater growth decline under the assumption of no fertilization effect of [CO_2] (the maximum growth decline was in the Mediterranean area, -50%). We must note that the results of Reyer et al., (2014) were obtained by averaging projections at 132 typical forest sites, which is a fundamental difference with our projections of growth changes that were conducted on in the whole European area on the 0.5° spatial resolution.

The FULL and STD versions of CASTANEA showed consistent trends in growth changes for all the European sub-regions. This result indicates that the representation of the environmental control of sink activity does not affect the qualitative predictions of the future of the European forest productivity previously obtained from NPP simulations and source-driven TBMs. The divergences between the averages of the growth anomalies predicted by the two CASTANEA

versions (Fig. 11, top plots) strongly varied among periods and sub-region. The FULL version predicted an increase in average annual wood growth that was approximately 10% greater than the STD version for the whole European area, under the assumption of a persistent [CO_2] fertilization effect, in period P2. This annual difference in wood growth may therefore result in important divergences in the prediction of the European wood stocks, when cumulated over the forest rotation period. The STD and FULL versions predictions were generally more consistent under the assumption of no long-term [CO_2] fertilization effect. However, the absolute differences between the STD and FULL anomalies were greater than 10% in a substantial part of the territory of all the sub-regions, regardless of the assumption made about the [CO_2] fertilization effect (Fig. 11, bottom plots). This result is caused by a higher sensitivity of the FULL version to the environmental gradients that affected forest functioning on the sub-regional scale. Within a given sub-region, the FULL model version therefore predicted higher growth in non-constraining areas but more pronounced growth declines at constraining sites. The more contrasted spatial pattern of the growth changes that was predicted by the FULL version (Fig. 10) indicated that the simulations were more affected by the local environmental factors, such as SWHC and local climate. Consistently, the spatial fluctuations in the growth changes that were predicted by the FULL version were more affected by the corresponding fluctuations of the soil water stress index (Fig. 12), which accounted for the local fluctuations of the SWHC and water balance. By contrast, the STD version of CASTANEA, which is a typical C-source TBM, was more impacted by the climate gradients that occurred on the continental scale (Fig. 10). We report that, for the middle of the next century (period P1), the representation of the sink control of forest growth affected the projections as much as the uncertainty associated with the C scenario emission and to the long-term fertilization effect of elevated [CO_2] (Fig. 13). Although the relative importance of the sink control on growth projections remain substantial in period P2 (15%), it declined because of the strong divergences among the climate scenario and expected [CO_2] values. This make the representation of the sink control on wood growth an important challenge for modellers. Overall, we found that the current generation of TBMs underestimates the spatial heterogeneity of the effects of climate change on forest growth that arise from the environmental limitation of the sink activity. A more complete representation of the processes that drive forest growth is needed in TBMs if they are to help defining regional management guidelines and forest policies (Böttcher et al., 2012).

5 Supplementary data

5.1 Calculation of the standing above ground woody biomass at the IFN sites

We first calculated the under-bark circumference at breast height (CBH_{ub}) from the measured over-bark circumference at breast height (CBH_{ob}), using bark coefficients (BC) reported in Table S1.1 (Eq. S1.1).

$$CBH_{ub}(t,n) = CBH_{ob}(t,n) \times BC \qquad \text{(S1.1)}$$

The CBHs of the year (n-5) were then inferred (Eq. S1.2) using the 5-year radial increment under bark (ri5).

$$CBH_{ub}(t,n-5) = (CBH_{ob}(t,n) \times BC) - 2 \times \pi \times ri5 \qquad \text{(S1.2)}$$

The total heights (H) of all the trees in the year (n-5) were obtained by retrieving 1 m to the measured total heights (Eq. S1.3).

$$H(t,n-5) = H(t,n) - 1 \qquad \text{(S1.3)}$$

5.1.1 Temperate oaks, F. sylvatica and P. abies

The total above-ground tree volumes (VTOT) in year (n) and (n-5) were calculated (Eq. S1.4 and S1.5) from CBH and H using the equations described in Vallet et al., (2006).

$$VTOT(t,n) = f(CBH_{ub}(t,n), H(n)) \qquad \text{(S1.4)}$$

$$VTOT(t,n-5) = f(CBH_{ub}(t,n-5), H(t,n-5)) \qquad \text{(S1.5)}$$

The stand volumes in year (n) and (n-5) were then calculated (Eq. S1.6 and S. 1.7) using the relative weight (w) attributed to each tree during the forest inventory (Charru et al., 2012).

$$\mathrm{VTOT(n)} = \sum_{t=1}^{tot} \mathrm{VTOT(t,n)} \times \mathrm{w(t)} \qquad \text{(S1.6)}$$

$$\mathrm{VTOT(n-5)} = \sum_{t=1}^{tot} \mathrm{VTOT(t,n-5)} \times \mathrm{w(t)} \qquad \text{(S1.7)}$$

We finally calculated the average annual above-ground woody biomass increment (AWBI) using Eq. S1.8. We assumed 50% of carbon content in dry matter (CARB=0.5) and species-specific density (DENS) reported in Table S1.1.

$$AWBI = \frac{(VTOT(n) - VTOT(n-5)) \times DENS \times CARB}{5} \qquad \text{(S1.8)}$$

Species	Wood density ($g.dm^{-3}$)	Bark coefficient (unitless)
Temperate oaks	650	0.87
F. sylvatica	600	0.90
P. abies	400	0.90
Q. ilex	-	0.90

Table S1.1: Wood density and bark coefficient used in the calculation of the standing above ground wood biomass.

5.1.2 Q. ilex

For *Q. ilex*, the calculation of the stand above-ground biomass followed a similar procedure (Eq. S1.9 to S1.13), but tree biomass (BIOM) was directly inferred from CBH using the equation of Rambal et al., (2004).

$$\mathrm{BIOM(t,n)} = f(\mathrm{CBH_{ub}(t,n)}) \qquad \text{(S1.9)}$$

$$\mathrm{BIOM(t,n-5)} = f(\mathrm{CBH_{ub}(t,n-5)}) \qquad \text{(S1.10)}$$

$$\mathrm{BIOM(n)} = \sum_{t=1}^{tot} \mathrm{BIOM(t,n)} \times \mathrm{w(t)} \qquad (1.11)$$

$$\mathrm{BIOM(n-5)} = \sum_{t=1}^{tot} \mathrm{BIOM(t,n-5)} \times \mathrm{w(t)} \qquad (1.12)$$

$$\mathrm{AWBI} = \frac{BIOM(n) - BIOM(n-5)}{5} \qquad (1.13)$$

We compared the calculated stand volumes and biomass to the values provided by the NFI for the year (n) in Fig. S1.5: note that we calculated total above-ground volume while IFN provide merchantable volumes (threshold diameter 7cm).

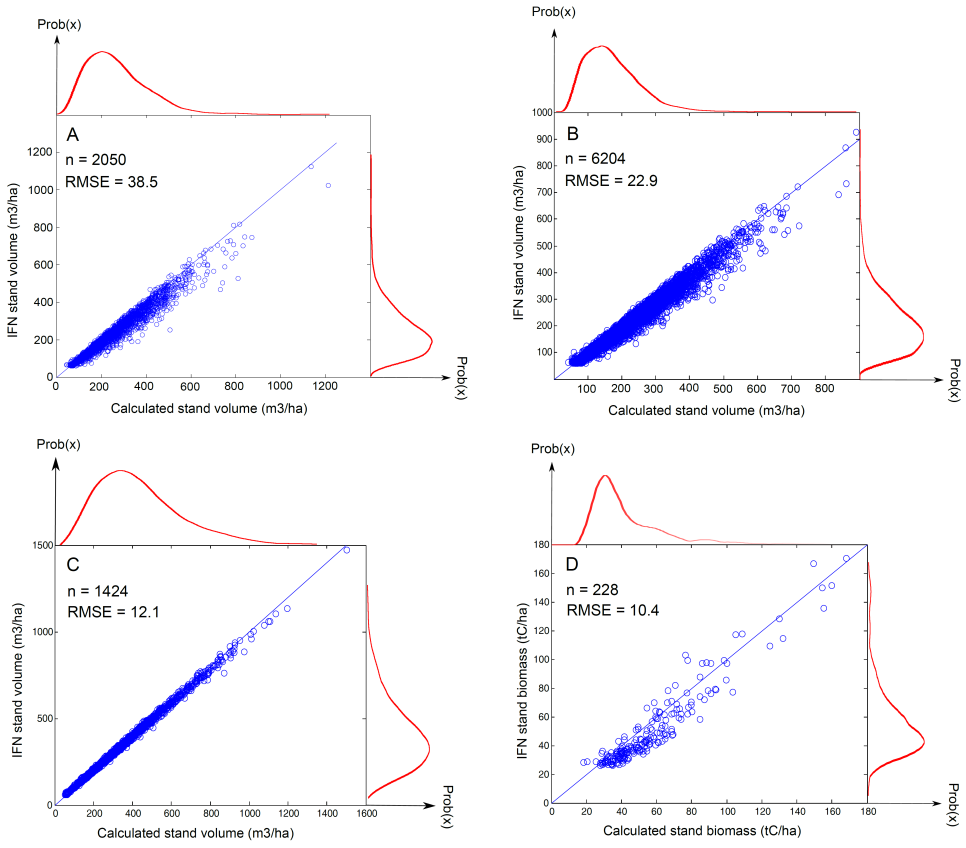

Figure S1.5: Comparison of the IFN volume (merchantable volumes) and the volumes calculated in this study (total volumes). A: *F. sylvatica*, B: Temperate oaks, C: *P. abies* and D: *Q. ilex*.

5.2 Spatial dependences of the FAPARmax measured at the IFN sites

Variable	Unit	Average	SD
X coordinate	m	718777.7	193054.2
Y coordinate	m	6627787.1	206721.4
age	year	96	41
stand basal area	m^2	27.2	11.9
slope	°	17.5	21.8
Soil water holding capacity	mm	145.9	51.8
mean temperature	°C	10.7	1.7
mean winter temperature	°C	8.5	1.8
Sum of the daily positive temperature over Mars to mid-April	°C	373.6	88.2
Sum of the daily positive temperature over mid-April to mid-May	°C	796.8	101.7
ETP	mm	748.7	93.1
Precipitation	mm	922.9	222.4
ETP during green season	mm	523.5	71.4
Precipitation during green season	mm	423.1	101.8
Soil water stress index (Guillemot *et al.*, 2015)	unitless	27.1	19.2
Soil water stress index during green season (Guillemot *et al.*, 2015)	unitless	25.2	18.1
P - ETP	mm	174.2	129.5
P – ETP during green season	mm	-100.4	30.2
Day of budburst	doy	120.9	8.2

Table S2.1: Description of the variables involved in the evaluation of the spatial dependences of the FAPARmax measured at the IFN sites.

5.3 Values of the pwood3 and pwood5 parameters

	pwood3 (unitless)	pwood5 (unitless)
Value	-0.014	-0.24

Table S3.1: Description of the variables involved in the evaluation of the spatial dependences of the FAPARmax measured at the IFN sites.

5.4 Prior and posterior distributions of the optimized parameters

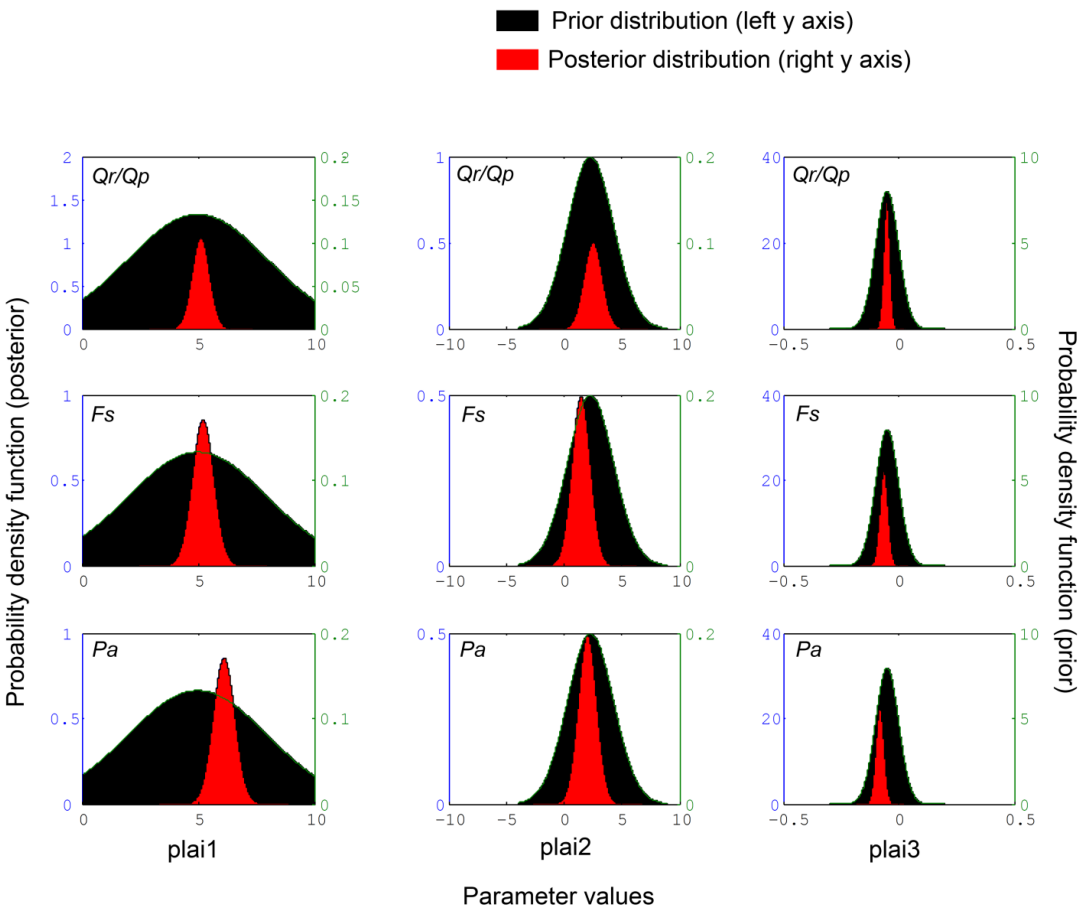

Figure S4.1: Results of the optimization of the LAImax sub-model. Units: plai (m^2leaf/m^2soil); plai2 (m^2leaf/m^2soil); plai3 (m^2leaf/m^2soil). Qr/Qp: temperate oaks; Fs: *F. sylvatica*; Pa: *Picea abies* .

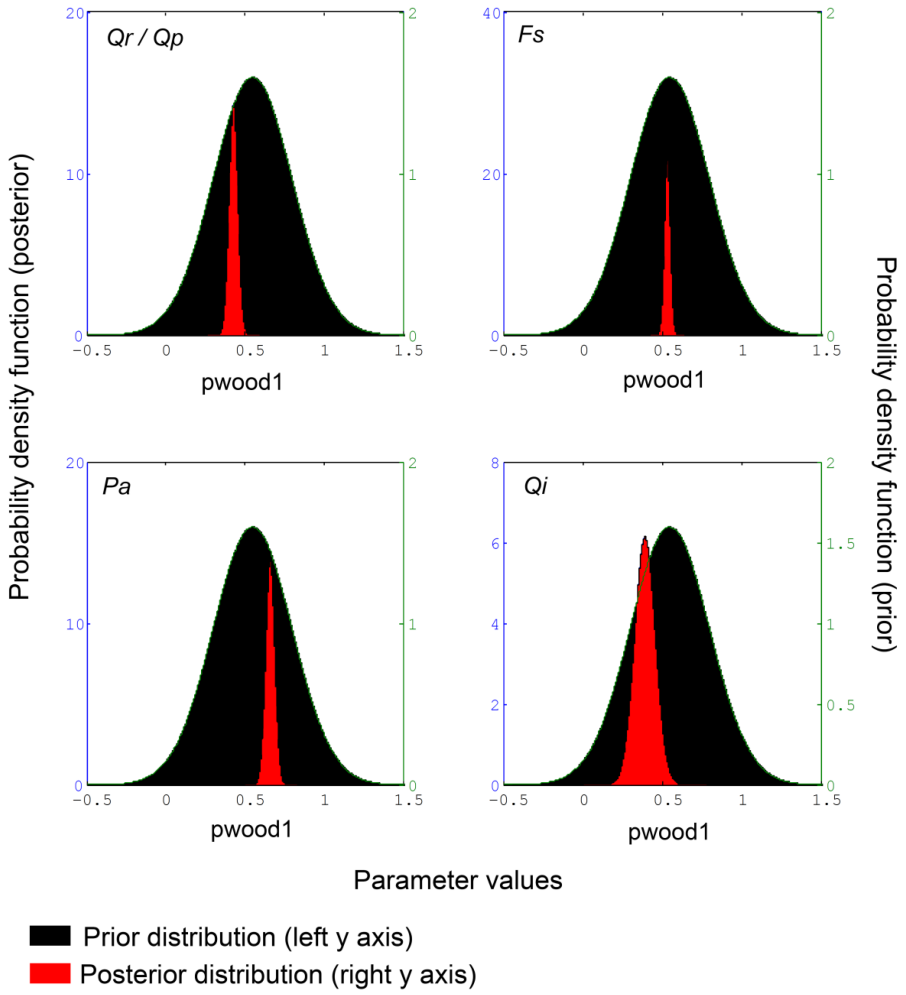

Figure S4.2: Results of the optimization of the wood allocation sub-model (CST version). Units: pwood1 (unitless). Qr/Qp: temperate oaks; Fs: *F. sylvatica*; Pa: *Picea abies*; Qi: *Q. ilex*.

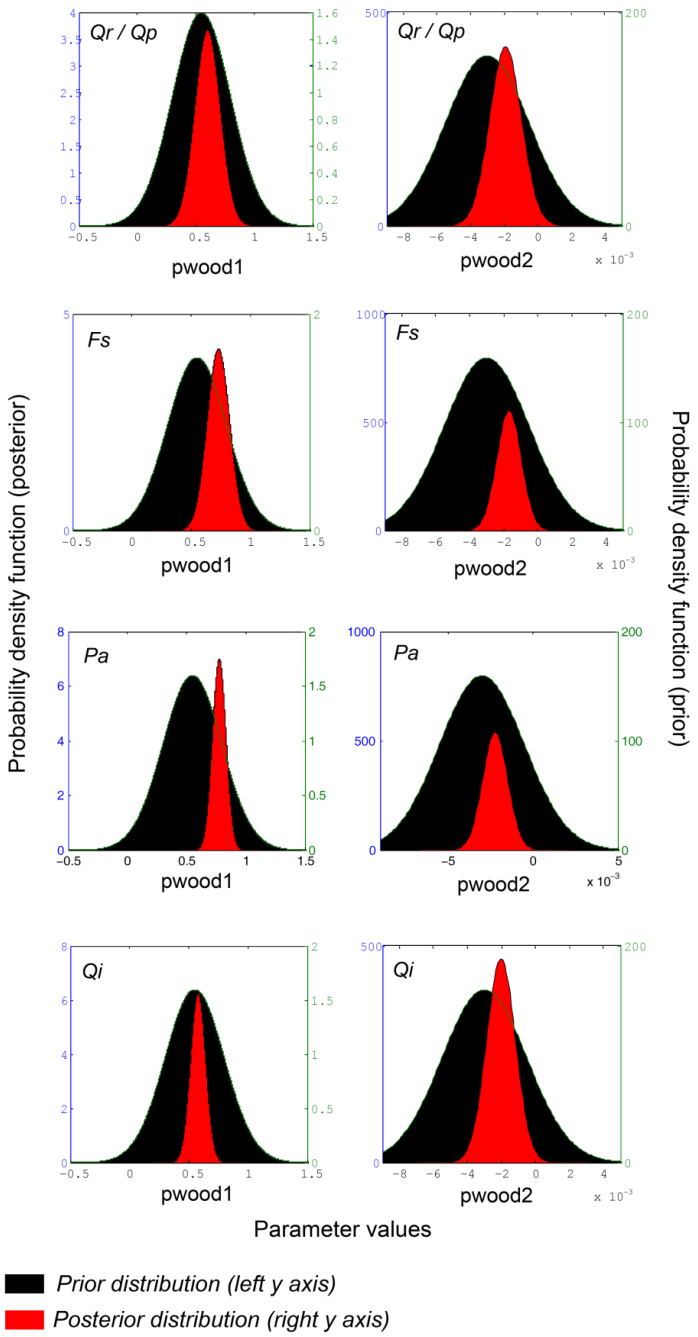

Figure S4.3: Results of the optimization of the wood allocation sub-model (STD version). Units: pwood1 (unitless); pwood2 ($year^{-1}$). Qr/Qp: temperate oaks; Fs: *F. sylvatica*; Pa: *Picea abies*; Qi: *Q. ilex*.

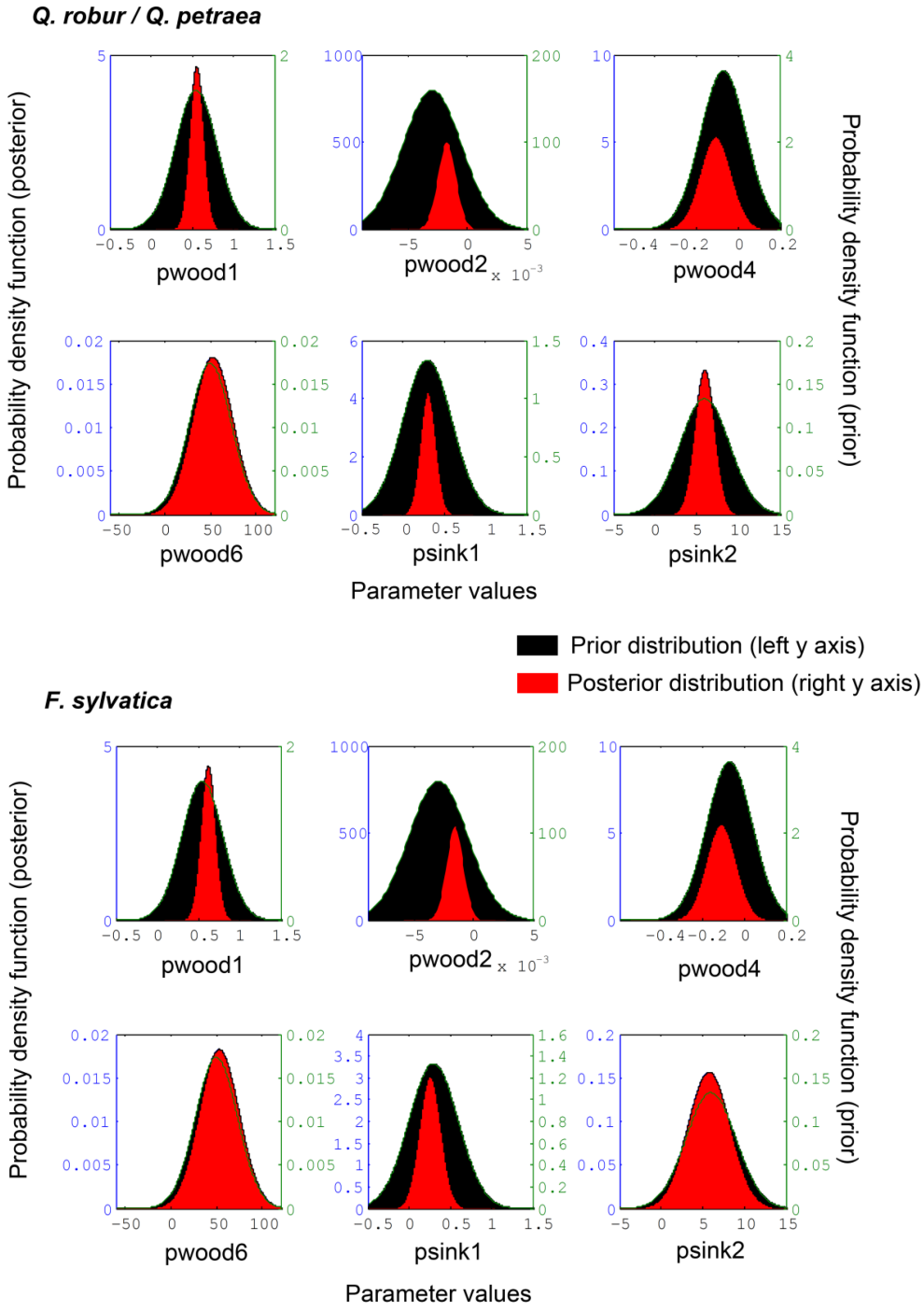

Figure S4.4: Results of the optimization of the wood allocation sub-model (FULL version). Units: pwood1 (unitless); pwood2 ($year^{-1}$); pwood4 (unitless); pwood6 (unitless); psink1 (unitless); psink2 (°C). Qr/Qp: temperate oaks; Fs: *F. sylvatica*; Pa: *Picea abies*; Qi: *Q. ilex*.

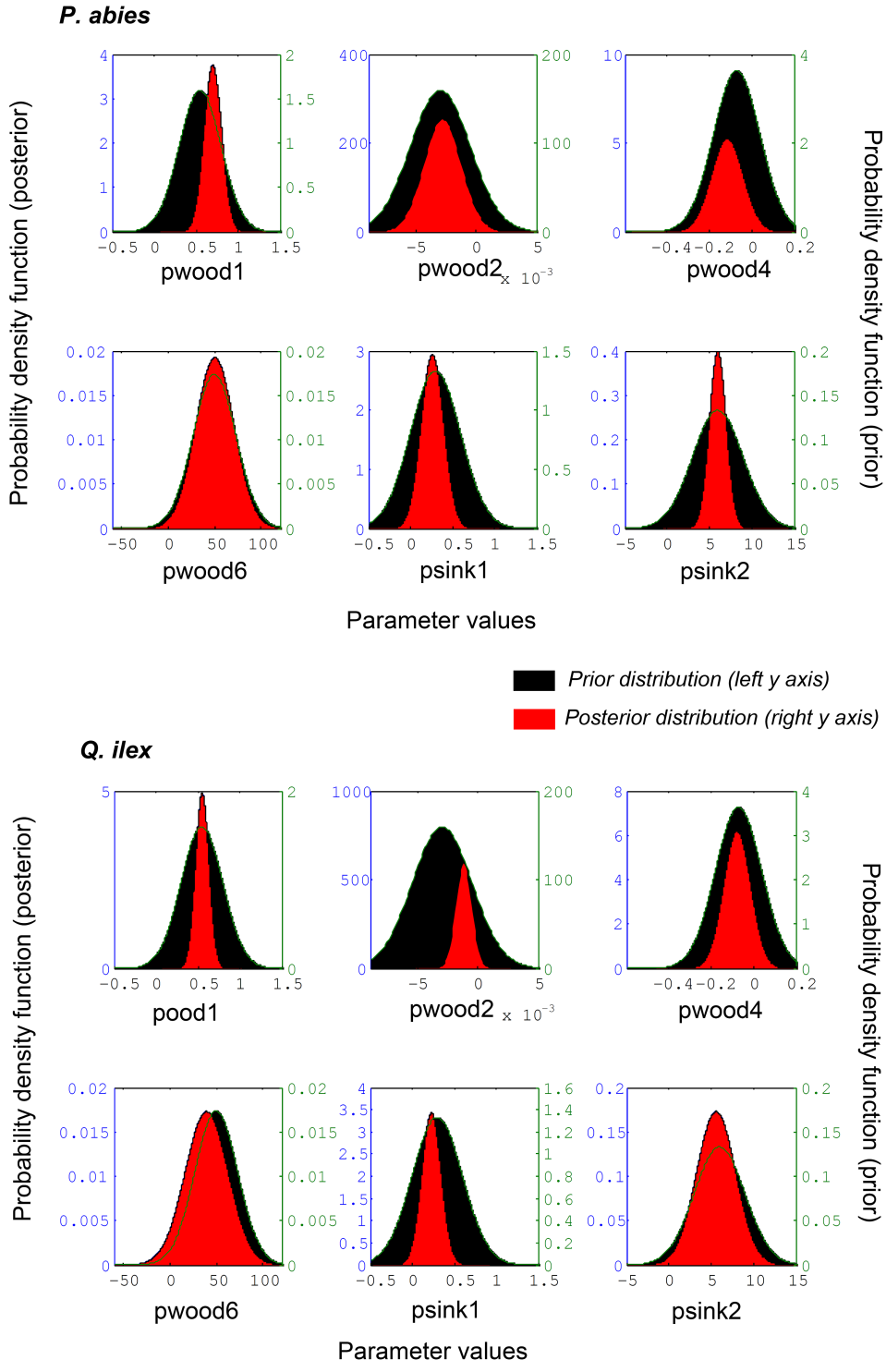

Figure S4.4: *(Continued)* Results for the optimization of the wood allocation sub-model (FULL version). Units: pwood1 (unitless); pwood2 ($year^{-1}$); pwood4 (unitless); pwood6 (unitless); psink1 (unitless); psink2 (°C). Qr/Qp: temperate oaks; Fs: *F. sylvatica*; Pa: *Picea abies*; Qi: *Q. ilex*.

5.5 Comparison of the GCM/RCM combination used in this study with six GCM/RCM combinations currently involved in the CMIP5 project

This section provides some Figures that illustrate that the climate projections of the MPI-ESM/RCA4 combination are representative of the projections of five GCM/RCM combinations currently involved in the CMIP5 project (Table S5.1). The comparison was conducted over the period 2075-2099 for the RCP8.5 C emission scenario.

Global Climate Model		**Regional Climate Model**		**ID of the GCM/RCM combination**
Institut	Model	Institut	Model	
Max-Planck-Insitut for Meteorology	*MPI-ESM-LR*	*Swedish Meteorological and Hydrological Institute*	*RCA4*	*SMHI (used in this study)*
EC-Earth consortium	EC-EARTH	Danish Meteorological Institute	HIRHAM5	DMI
EC-Earth consortium	EC-EARTH	Royal Netherlands Meteorological Institute	RACMO22	KNMI
Centre National de Recherches Météorologiques	CNRM-CM5	Météo France	Aladin52	CNRM
Laboratoire des sciences du climat et de l'environnement - Institut Pierre Simon Laplace	IPSL-CM5A	Laboratoire des sciences du climat et de l'environnement - Institut Pierre Simon Laplace	WRF331	IPSL
Max-Planck-Insitut for Meteorology	MPI-ESM-LR	CLM Community	CCLM4-8-17	CLMcom

Table S2.1: Description of the variables involved in the evaluation of the spatial dependences of the FAPARmax measured at the IFN sites.

More details about the GCMs and RCMs used in this comparisons and specific references can be found in Jacob et al., (2014) and Kotlarski et al., (2014). In the following, ensemble combination refers to the result obtained by averaging the projections of the 5 GCM/RCM combinations used for the comparison.

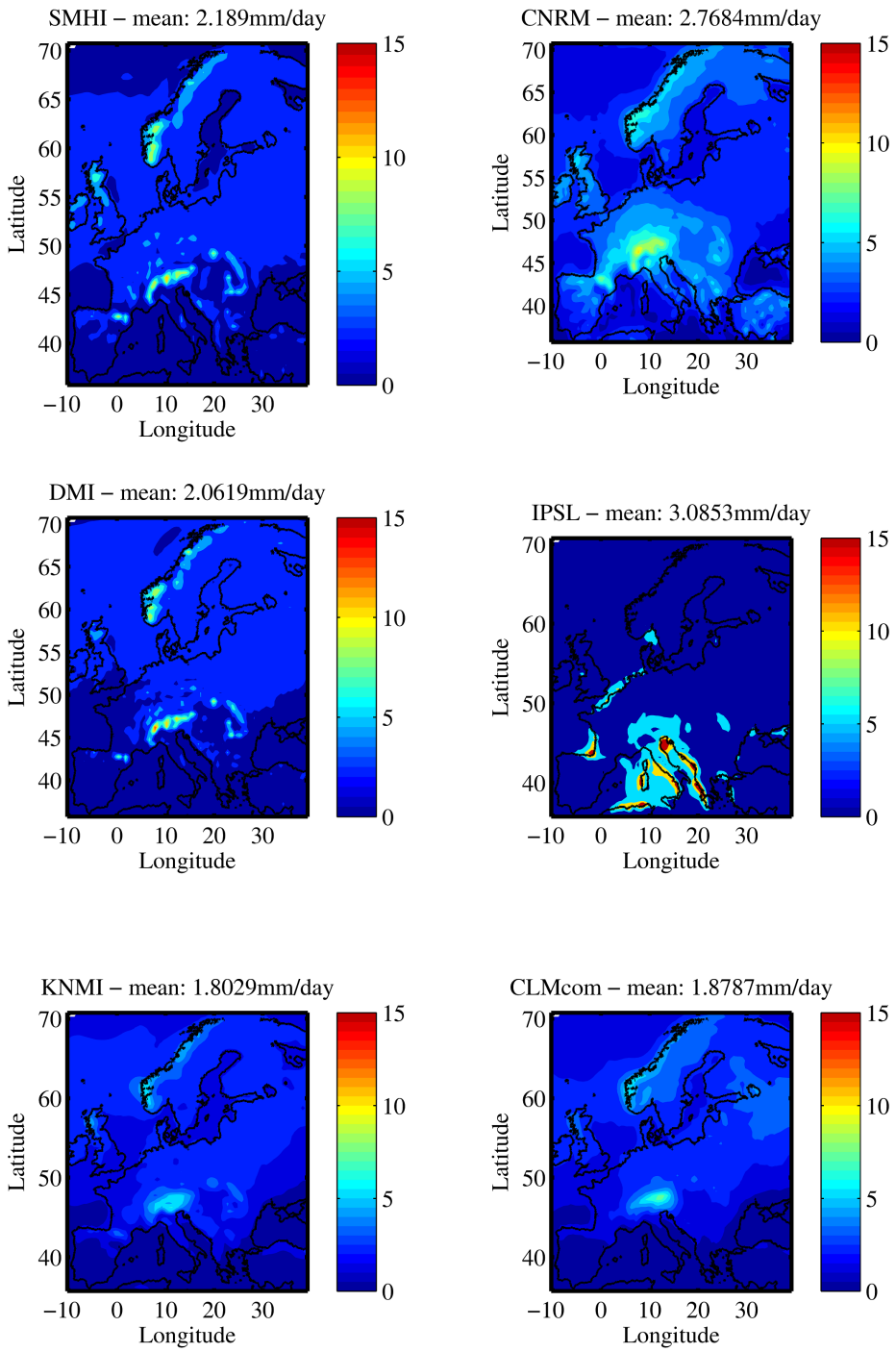

Figure S5.1: Mean daily precipitation of May, June, July and August over the period 2075-2099.

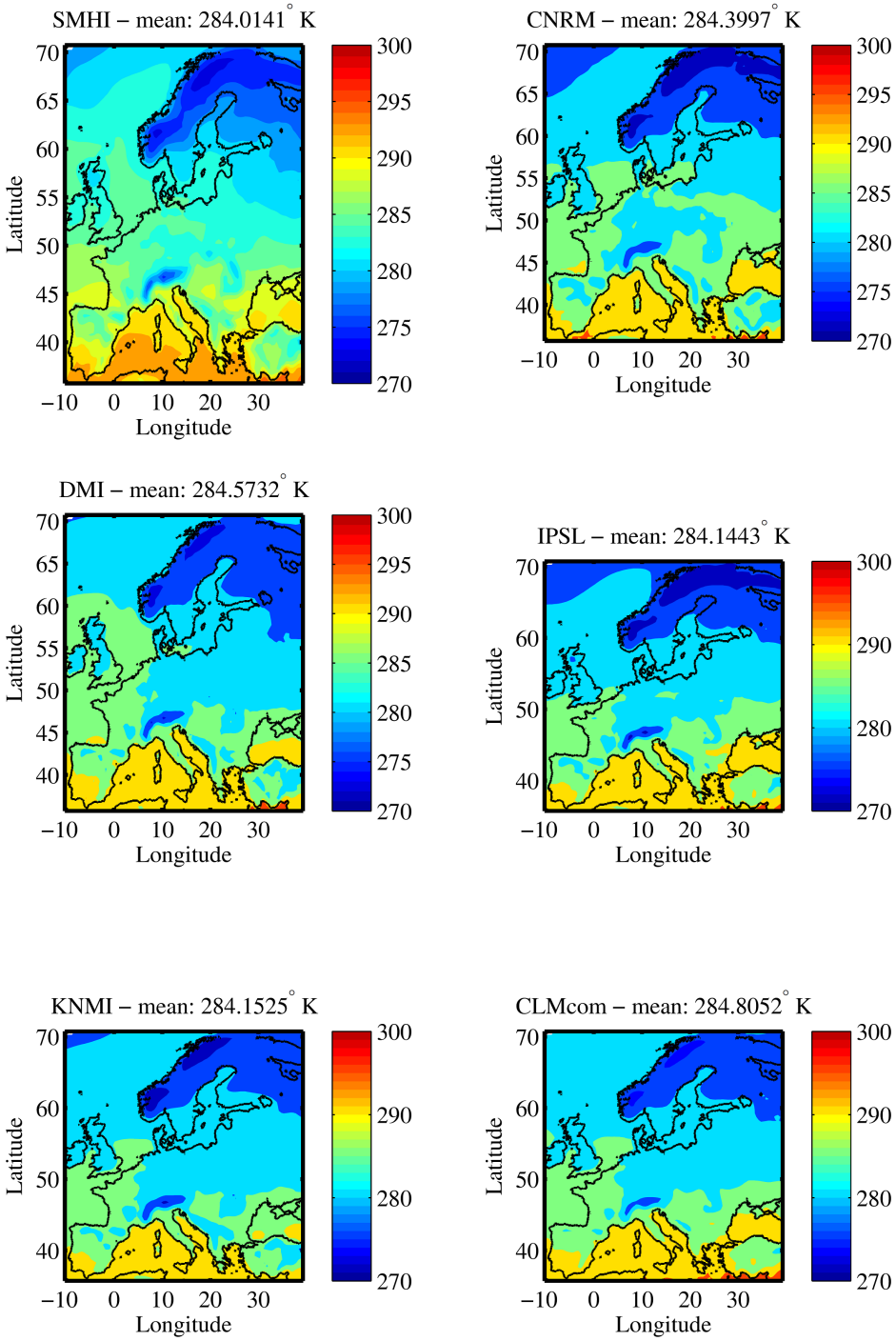

Figure S5.2: Mean daily precipitation of May, June, July and August over the period 2075-2099.

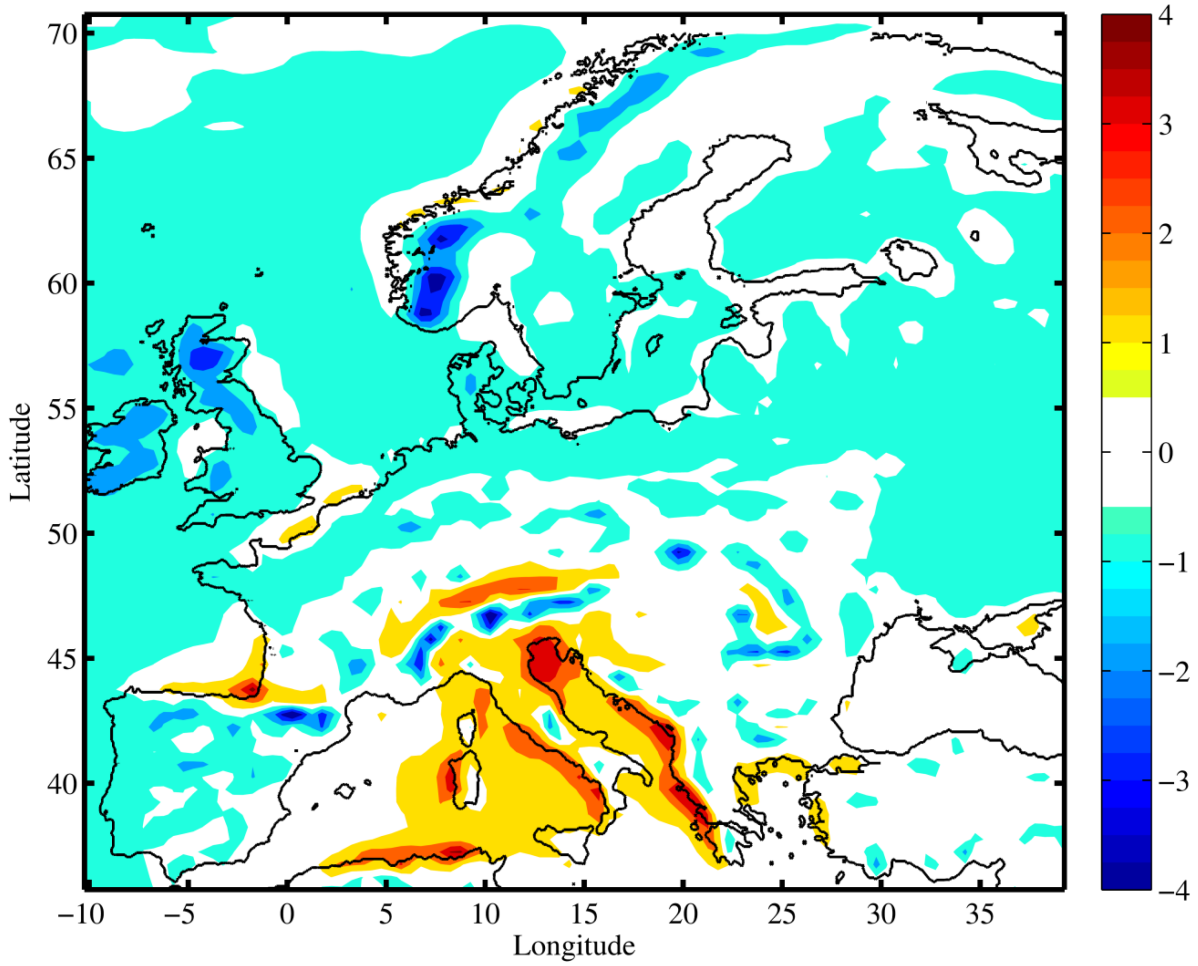

Figure S5.3: Difference between the SMHI combination and the ensemble combination for the daily precipitation of May, June, July and August over the period 2075-2099.

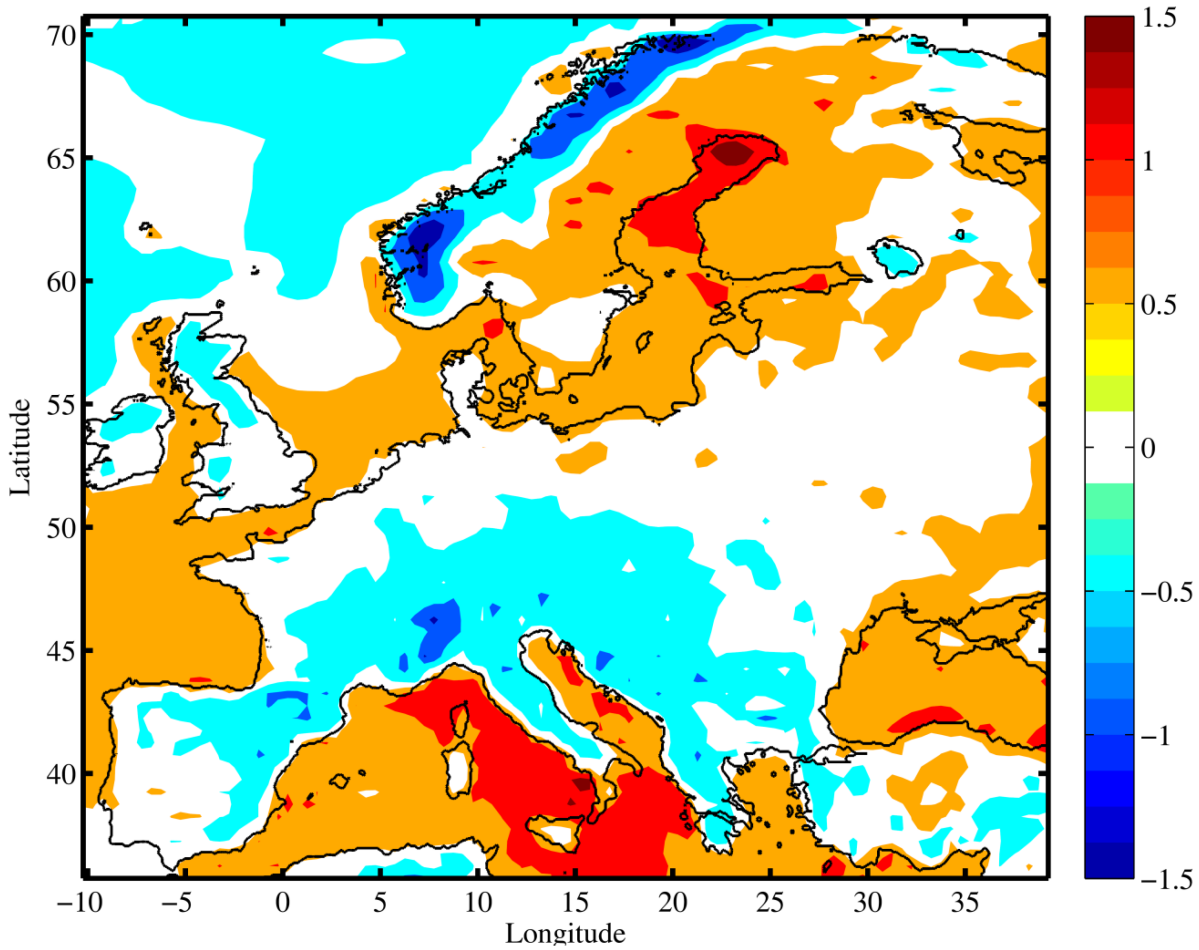

Figure S5.4: Difference between the SMHI combination and the ensemble combination for the mean annual temperature over the period 2075-2099.

5.6 Maps of the projected changes of wood growth in European forests under the C emission scenarios RCP2.6 and RCP4.5

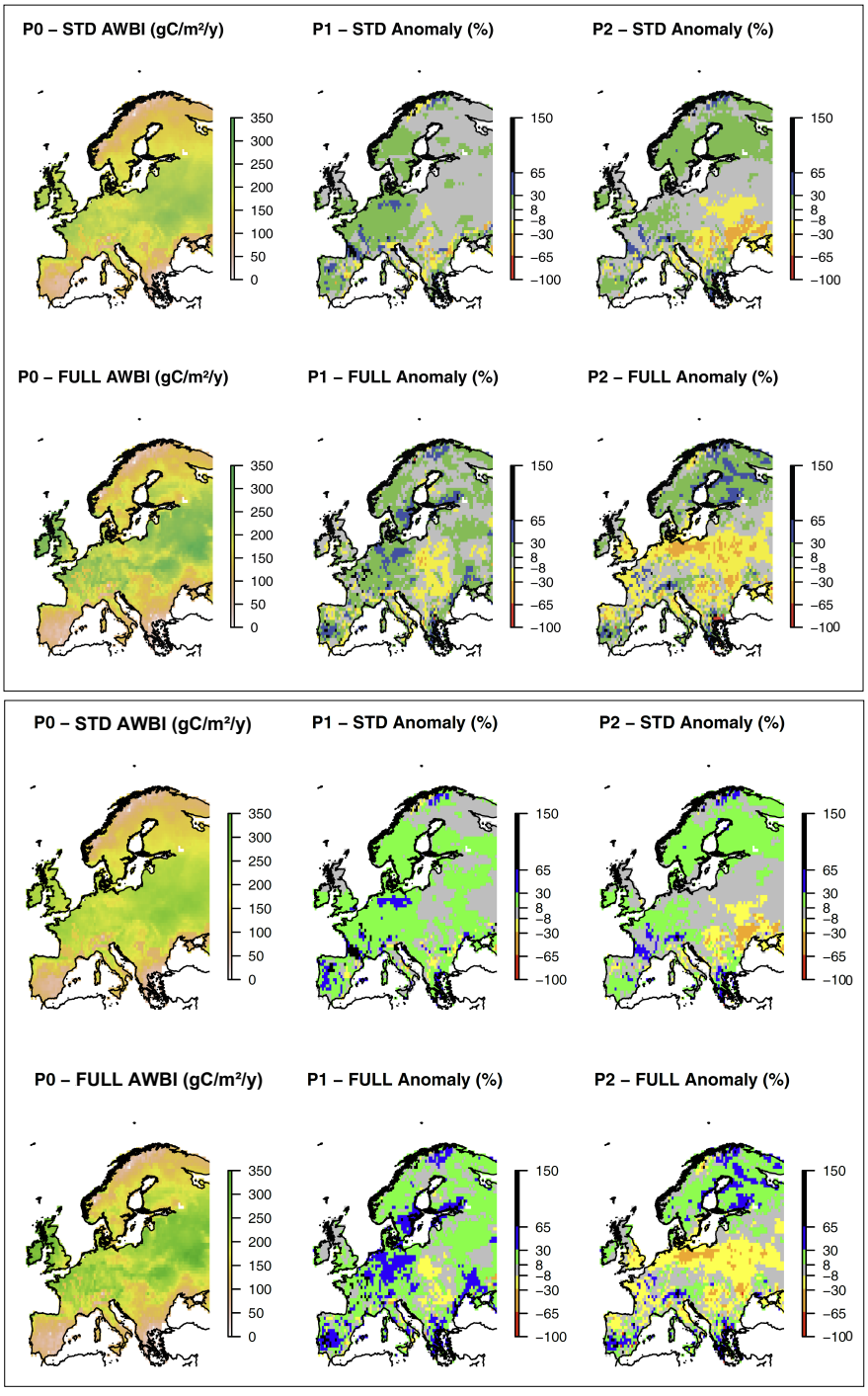

Figure S6.1: Maps of the projected changes of wood growth in European forests under the C emission scenarios RCP2.6. The simulation from the STD and the FULL version of CASTANEA are compared under the assumption of no $[CO_2]$ fertilization effect (top panel) and persistent $[CO_2]$ fertilization effect (bottom panel).

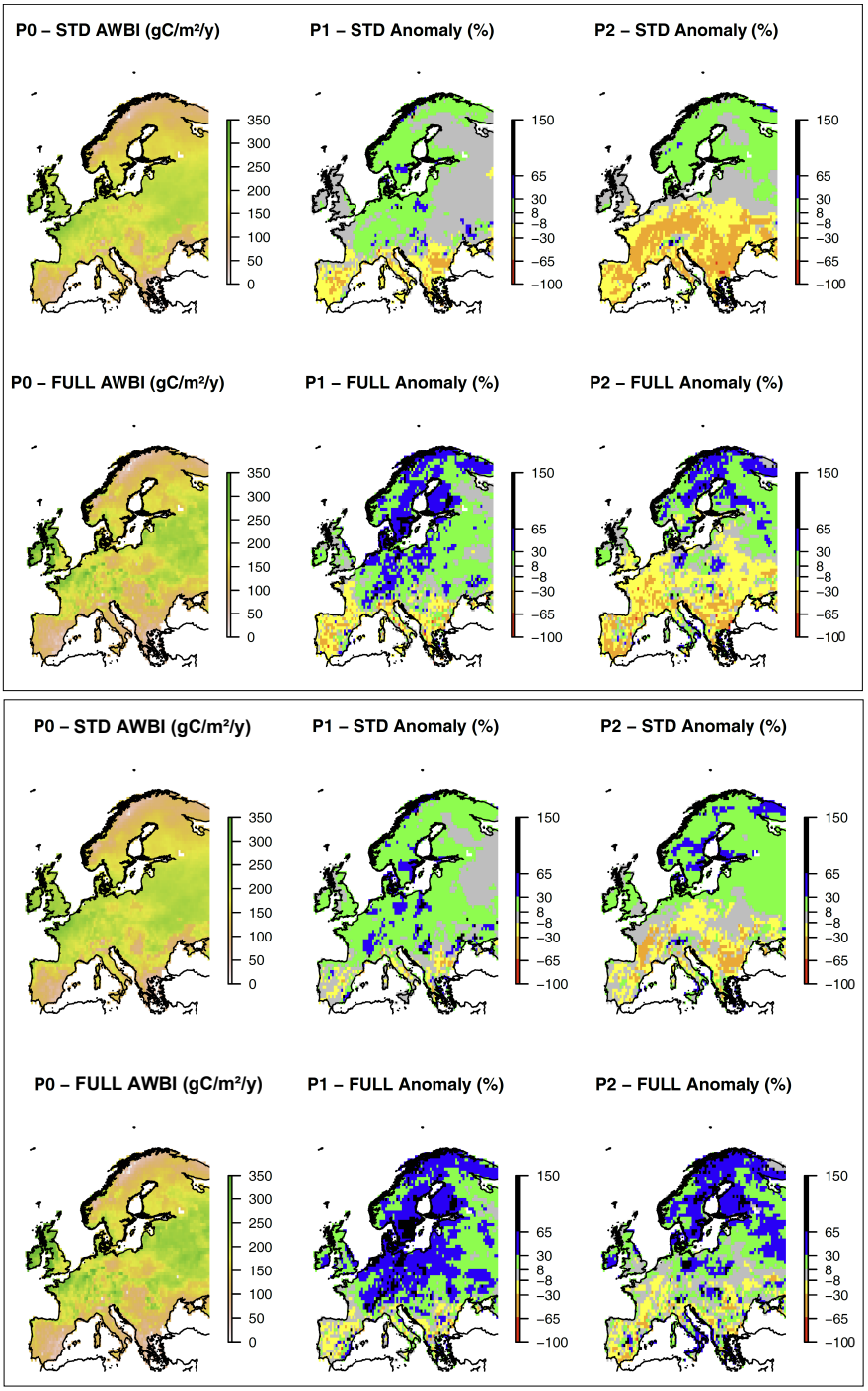

Figure S6.2: Maps of the projected changes of wood growth in European forests under the C emission scenarios RCP4.5. The simulation from the STD and the FULL version of CASTANEA are compared under the assumption of no $[CO_2]$ fertilization effect (top panel) and persistent $[CO_2]$ fertilization effect (bottom panel).

Chapter 4

Assessing the effects of management on forest growth across France: insights from a new functionnal-structural model

1 Introduction

The current increase in drought intensity and frequency (IPCC, 2014) has been recognized as a probable cause of forest dieback (e.g. Anderegg et al., 2012) and is expected to affect forests greatly worldwide (Allen et al., 2010; Lindner et al., 2010). The assessment and projection of climate change effects on forests often usegrowth as a surrogate for tree vitality (Bigler and Bugmann, 2003; Dobbertin, 2005). Indeed, growth has long been considered as an integrated signal of biotic and abiotic factors that reflect the functioning of the whole tree (Cook, 1985). Long-term low growth is a well-known trait of dying trees, and growth has been reported to be an important variable for tree mortality (Bigler and Bugmann, 2003) or species range (Benito-Garzón et al., 2013) projections. Long-term projections of forest stand growth under a rapidly changing environment is consequently an important modelling goal (Lara et al., 2013).

So far, projections of effects of climate change on forest growth have principally relied on ecophysiological process-based models (PBMs) validated at the stand rotation time scale (Pretzsch et al., 2008; Fontes et al., 2010). PBMs provide a framework to formalize biophysical hypotheses and combine knowledge about the physiological mechanisms that determine forest functioning and growth. PBMs can be evaluated at different temporal and spatial scales according to the process of interest (leaf or canopy matter and energy fluxes, stand or tree growth, or distributional range) and can therefore be used to investigate how tree functions will change in a changing environment (Mäkelä et al., 2000). Forest PBMs differ in their complexity, and one can separate stand PBMs that aimed to predict growth, or carbon (C) and water fluxes at the stand scale, from tree-centred PBMs that aimed to simulate the functioning of each individual tree within a forest stand (Fontes et al., 2010). A recent study, however, has demonstrated that more robust results are obtained at the stand scale when stand PBMs are used rather than aggregated predictions from tree-centred models (Cao, 2006). Moreover, tree-centred PBMs can hardly be used to simulate the long-term functioning of forests grown under contrasted conditions as they need a huge amount of data to be properly calibrated, and considerable computing power. As a consequence, few PBMs are able efficiently to simulate temporal changes in stand structure, i.e. changes in the distribution of the tree size features. In particular, most of them fail to predict the circumference and volume increments of the individual trees, as well as the evolution of tree density during the forest rotation.

However, the structure of forest stands has strong effects on the functioning of individual trees, through size and competition (Gomez-Aparicio et al., 2011). Competition intensity has been shown to modulate the stand growth responses to annual climate (Piutti and Cescatti, 1997; Magruder et al., 2013), and tree growth responses to environmental factors may be strongly affected by individual size (DeLuis et al., 2009; Mérian and Lebourgeois, 2011). Competition is also a major process involved in climate-driven forest dieback and mortality (Linares et al., 2010; Ruiz-Benito et al., 2013). These results suggest that silviculture, which controls the amount and distribution of available growing space in a stand,is of major importance for the mitigation of climate change effects on forests (Keenan, 2012; Vayreda et al., 2012). The inability of most stand PBMs to simulate stand structure consequently strongly limits their explorative capacity and their potential applications. First, they are not suitable for simulating the influence of forest management on forest functioning, precluding (1) the assessment of biomass stocks and sink capacities of the increasingly managed part of the world's forests (Bellassen et al., 2011a) and (2) the design of adaptive silvicultural guidelines taking into account current and future impacts of climate change. Secondly, stand PBMs without stand structure representation cannot be directly evaluated (i.e. without strong upscaling hypotheses) with the most abundant available data in forest science, namely dendrometric measurements from forest inventories (tree density or basal area) and dendrochronological series. The simulation of the stand structure would therefore allow modellers to formalize and to test functional hypotheses on the determinism of growth at larger time and spatial scales, e.g. along contrasted regional or continental gradients. Finally, stand PBMs usually cannot accurately simulate processes intimately related to competition and stand structure, such as tree mortality (Bigler and Bugmann, 2003; McDowell et al., 2011) or productivity decline of aged stands (Binkley et al., 2002; Caspersen et al., 2011).

As a consequence, few recent attempts have been made to simulate the dynamics of forest structure within PBMs. Grote et al. (2011) complemented the MoBiLE-PSIM model with routines for average dimensional tree growth to improve the simulated C balance. Wang et al. (2011) simulated the impact of thinning on a coniferous forest within the TRIPLEX model using empirical prediction of the tree size distribution characteristics. In another approach, PBMs were coupled with empirical tree growth models to simulate the size trajectories of all the trees of a forest stand (Bellassen et al., 2010; Mäkelä et al., 2013; Poschenrieder et al., 2013). In a national-scale study, Bellassen et al. (2010) incorporated the fundamental rules

of tree growth competition exposed in Dhôte (1999) into the global-scale PBM ORCHIDEE (Krinner et al. 2005). This work has been developed over a broad plant functional type. For this reason, it has two clear limits in that (1) it shows moderate agreement with observed data of forest productivity (Babst et al., 2013) and (2) it precludes accessing information on contrasted species-specific changes in stand structure (Knowles and Grant, 1983). In contrast to the PBM approach, empirical tree-centred growth models proved their ability to predict temporal changes in forest structure on a purely statistical basis (Burkhart and Tomé, 2012). The way resources are distributed among the individual trees, which is related to the tree growth performances (Nord-Larsen et al., 2006; Weiner and Damgaard, 2006), is the focal point of these models. Distribution of resources depends on the mode of tree competition (Weiner, 1990), which can be either size symmetric (i.e. growth is proportional to the size) when below-ground resources are limiting or size asymmetric when growth is predominantly limited by light (Schwinning and Weiner, 1998). Recent studies reported that the mode of competition can vary spatially, along ecological gradients (Pretzsch and Biber, 2010), but also temporally (Metsaranta and Lieffers, 2010; Zang et al., 2011). This fluctuation of the growth size asymmetry could thus be an important driver of the stand structure (Hara, 1988; Metsaranta and Lieffers, 2008) which is poorly considered in empirical tree-centred growth models. Previous studies conducted at both spatial and temporal scales reported a strong positive correlation between growth size asymmetry and productivity that can benefit tree-to-tree competition modelling (Pretzsch and Biber, 2010). Importantly, these empirical models cannot be used to project future impacts of climate change on a forest because they only seek to describe the statistical relationship among data, with no insight into the underlying, generalizable processes (Korzukhin et al., 1996). In this study, our goal was to simulate the long-term temporal changes in stand structure of deciduous forests within a process-based model. We present CASTANEA-SSM, a new functional structural plant model based on the coupling of the species-specific stand PBM CASTANEA with an empirical tree-centred module of growth competition (this stand structure module is hereafter referred to as SSM). Our modelling approach aimed to predict the size trajectories of every tree of a given stand during the forest rotation. Forest management has been considered by integrating a thinning-induced mortality algorithm at the tree level. The transient effect of thinning on canopy development, which can strongly affect tree water relations (Bréda et al., 1995; Rodriguez-Calcerrada et al., 2011), was assessed thanks to a new module of annual maximum leaf area index temporal dynamic. After calibrating the SSM through a thorough

analysis of the spatial and temporal variability of the mode of competition, we evaluated the fully coupled CASTANEA-SSM model over France for common beech (*Fagus sylvatica*) and temperate oak species (*Quercus petraea* and *Quercus robur*). Finally, we used the evaluated model to assess the potential of management practices to affect forest functioning at the country scale, by comparing the effect of contrasted silvicultural practices on simulated stand atmosphere C fluxes and growth.

2 Materials and Methods

2.1 Model structure: the CASTANEA PBM

The ecophysiological multilayer PBM CASTANEA (Dufrêne et al., 2005) was used to simulate the annual stand growth of the study sites. CASTANEA aims at simulating C and water fluxes and stocks of an even-aged monospecific forest stand at the rotation time scale. Briefly, the stand simulated by CASTANEA comprises four functional compartments: foliage, woody biomass (including stem, branches and coarse roots), fine roots and the pool of carbohydrate reserves. The canopy is considered homogeneous horizontally and vertically sub-divided into a given number of layers, each of them enclosing a constant amount of leaf area. One of the major strengths of the model (Keenan et al., 2012a) is its ability to reproduce the interannual fluctuations of C fluxes over Europe (Delpierre et al., 2012). A complete description of CASTANEA is given in Dufrêne et al. (2005), with subsequent modifications from Davi et al. (2009) and Delpierre et al. (2012). The variation in annual maximum leaf area index (LAI_{max} of a given year is not only simulated according to seasonal climate (previous version), but also as a function of a soil water stress index (SWS_{index}, see CASTANEA: soil water stress index in the Supplementary Data) defined on the previous year. The LAI_{max} value decreases when the SWS_{index} of the previous year is high, and increases otherwise. A maximum bound value of LAI_{max} is determined by an envelope curve depending on stand age. Additionally, the LAI_{max} value is reduced in the case of low carbohydrate reserve to prevent complete depletion of carbohydrate reserves (see CASTANEA: inter-annual variation of LAI_{max} in the Supplementary Data). Carbon allocation to wood growth is determined annually as a fraction of gross primary productivity using allocation coefficients. Allocation coefficients are related to stand age, as well as to the current and previous year water stress (see CASTANEA: inter-annual variation of wood growth in the Supplementary Data).

The module of C allocation to wood growth was preliminarily calibrated on RENECOFOR tree ring series (over the 1970-1990 period) to simulate the averaged above-ground biomass increment across stands.

2.2 Model structure: the empirical stand structure module (SSM)

The structure of the SSM is strongly inspired by the empirical tree-centred yield model FAGACEES (LeMoguédec and Dhôte 2011). The SSM works at a yearly timescale. It simulates (1) the distribution of the stand volume increment in a distribution of individual trees and (2) the mortality of individual trees (Fig. 1) resulting either from self-thinning or from commercial thinning, in the case of a managed stand. Individual tree growth simulation relies on the following function (Deleuze et al., 2004; Fig. 1):

$$\begin{aligned} \mathrm{BAI}_i &= \frac{\gamma_{\mathrm{sim}}}{2} \\ &\times \left[\mathrm{CBH}_i - m\sigma_{\mathrm{sim}} + \sqrt{(m\sigma_{\mathrm{sim}} + \mathrm{CBH}_i)^2 - (4\sigma_{\mathrm{sim}} \times \mathrm{CBH}_i)} \right] \end{aligned} \tag{1}$$

where $\mathrm{CBH_i}$ is the circumference at breast height of a given tree i and $\mathrm{BAI_i}$ is its corresponding annual basal area increment. In this relationship, only trees with a circumference at breast height (CBH) above the threshold σ_{sim}, which can be interpreted as the minimum circumference for direct access to sunlight, have a significant growth. Overstorey trees then grow proportionally to their size, following a slope coefficient g sim (Fig. 1). m is a smoothing parameter. Natural tree mortality occurs when the stem density of the stand (N) exceeds the maximum density ($\mathrm{N_{max}}$) allowed by the stand quadratic mean diameter ($\mathrm{D_g}$):

$$N_{\mathrm{max}} = \frac{\alpha_s}{D_{\mathrm{g}}^{\beta_s}} \tag{2}$$

where α_S and β_S are species-specific parameters (Charru et al., 2012) and

$$D_g = \sqrt{\frac{\frac{1}{4\pi}\sum_{N}^{i=1} CBH_i^2}{N}} \tag{3}$$

Based on these relationships, the relative density index (RDI; Reineke, 1933) is defined as the ratio of actual to maximum density:

$$RDI = \frac{N}{N_{max}} \tag{4}$$

The RDI values range within the [0,1] interval. Self-thinning (i.e. the mortality of the smallest trees) occurs when RDI = 1. In managed stands, RDI is strongly modulated by intermediate thinning (Supplementary Data Fig. S1). In SSM, silvicultural scenarios are characterized by two parameters: $RDI_{initial}$, the target RDI when the age of the stand is 0, and RDI_{final}, the target RDI at the end of the stand rotation. Throughout the rotation, RDI is kept close to the RDI target value (Supplementary Data Fig. S1), with

$$RDI_{target} = \frac{RDI_{final} - RDI_{Initial}}{age_{final}} \times age + RDI_{initial} \tag{5}$$

where age is the current age of the stand and age_{final} is the stand age at the end of the rotation. The RDI is allowed to vary around RDI_{target} within a constant interval determined by RDI_l : when RDI reaches $RDI_{target} \times (1 + RDI_l)$ the stand is thinned to $RDI_{target} \times (1 - RDI_l)$ (RDI_l is fixed to $0.2 \times RDI_{target}$, see Supplementary Data Fig. S1). Final commercial cutting occurs when the age of the stand reaches age final or when the mean CBH of the stand rises above a given value. The thinning-induced modification of the tree distribution is determined by a probabilistic harvest sub-module (Bellassen et al., 2010). In this approach, each tree is given a probability of cutting determined by P_{min}, P_{max} and T_{strat}, corresponding to the minimum and maximum probabilities of cutting and the thinning strategy index, respectively. T_{strat} determines which CBH classes are to be preferentially thinned, allowing for a wide panel of silvicultural scenarios. After cutting, harvested volume is calculated and the thinning intensity

(τ_h) is determined as:

$$\tau_h = \frac{vol_{thin}}{vol_{tot}} \tag{6}$$

where vol_{thin} and vol_{tot} are the thinned volume and the total volume, respectively. The harvest sub-module is fully described in the supplementary information.

2.3 Model structure: coupling methodology

The annual stand biomass increment prediction from CASTANEA is first converted to stand volume increment (see Above ground volume calculation in the Supplementary Data) and then used as an input in the SSM, where it is disaggregated among a distribution of individual trees (Fig.1).

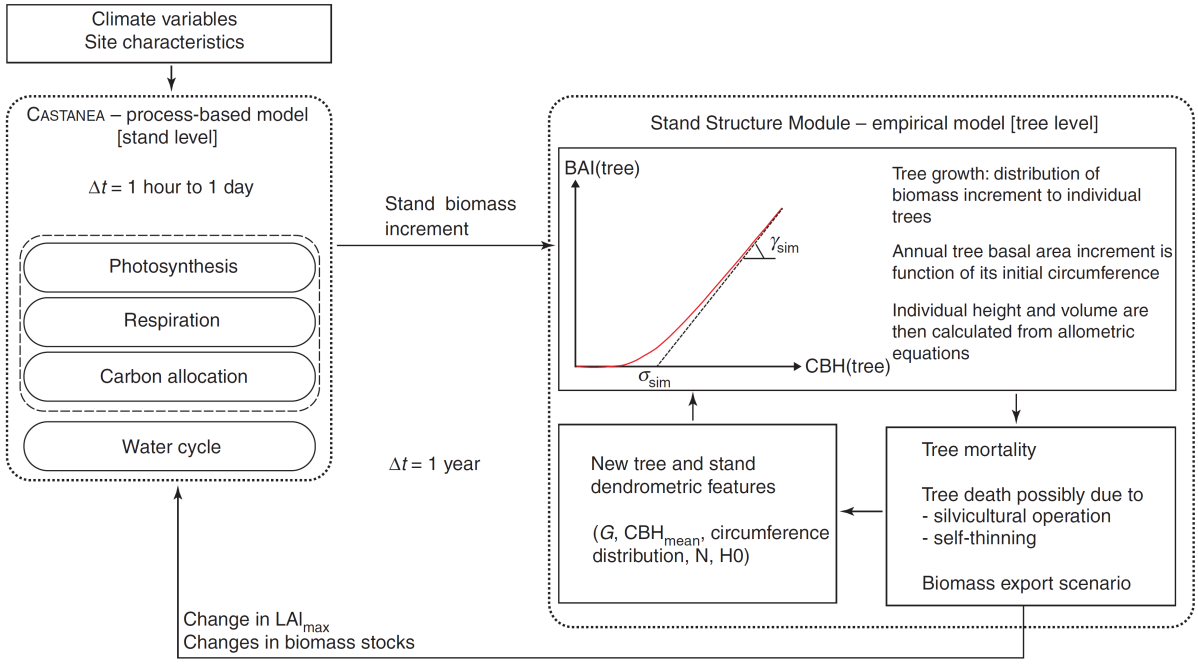

Figure 1: Conceptual diagram of the coupled CASTANEA-SSM. Abbreviations: σ_{sim} and γ_{sim} are parameters [see eqn (1)]; G, stand basal area; CBH_{mean}, mean stand CBH, N, stand stem number; H0, top height; circ., circumference; BAI, basal area increment.

To ensure consistency between individual tree growth and stand volume increment, σ_{sim} and γ_{sim} [from eqn (1)] are annually adjusted (see Modelling of the changes in stand structure in the Supplementary Data) so that the sum of the individual volume increment (calculated from basal area increments and initial CBHs) matches the stand-level prediction. At each occurrence of

a thinning event, changes in LAI_{max} and biomass stocks are updated in CASTANEA for the next simulation (Fig. 1). Biomass stocks are reduced by $100\tau_h\%$ [see eqn (6)]. LAI_{max} for a given year, y, is determined by the following equation (see CASTANEA: inter-annual variation of LAI_{max} in the Supplementary Data):

$$LAI_{thin}(y) = \frac{LAI_{max}(y)}{a_{LAI} + b_{LAI}100\tau_h} \quad (7)$$

where LAI_{max} and LAI_{thin} are the potential stand LAI_{max} and the actual stand LAI_{max} after thinning, respectively. a_{LAI} and b_{LAI} are species-specific parameters (Table 1).

Parameter	Description	Value (beech/oak)	Units	Equation	Reference
σ_{sim}	Significant growth threshold	See the Results	cm	1	–
γ_{sim}	Slope of the linear part of the relationship	See the Results	cm years^{-1}	1	–
m	Smoothing parameter	1·05	Unitless	1	Deleuze *et al.* (2004)
α_s	Parameter of self-thinning equation	14 / 13·68	Trees ha^{-1}	2	Le Moguédec and Dhôte (2011)
β_s	Parameter of self-thinning equation	1·7/1·57	Trees ha^{-1} ln(cm)$^{-1}$	2	Le Moguédec and Dhôte (2011)
$RDI_{initial}$	Target RDI at age = 0	See the Materials and Methods	Unitless	5	–
RDI_{final}	Target RDI at age = age_{final}	See the Materials and Methods	Unitless	5	–
age_{final}	Age at the end of the stand rotation	150	Years	5	Lanier *et al.* (1994)
P_{min}	Minimum relative mortality rate	0·01	Unitless	S9	Bellassen *et al.* (2010)
P_{max}	Maximum relative mortality rate	0·05	Unitless	S9	Bellassen *et al.* (2010)
T_{strat}	Thinning strategy index	1	Unitless	S9	Bellassen *et al.* (2010)
a_{LAI}	Coefficient for the thinning effect on LAI	1·057/1·09	Unitless	7	E. Dufrêne, unpubl. res.
b_{LAI}	Coefficient for the thinning effect on LAI	0·016/0·018	Unitless	7	E. Dufrêne, unpubl. res.

Table 1: Description of the SSM parameters; where values are different for beech and oak these are indicated

CASTANEA-SSM allows for different scenarios of biomass exportation following thinning. Then on-exported biomass goes to the litter compartment.

2.4 Study sites and field measurements

Long-term growth and physiological data were obtained from the French permanent plot network for the monitoring of the forest ecosystem (RENECOFOR, which is part of the ICP Forest Level II program; Ulrich, 1997). The dataset included measurements from 14 forest sites of common beech and 18 forest sites of temperate oak species (16 and two *Q. petraea* and *Q. robur* forest sites, respectively) distributed over mainland France (Fig. 2).

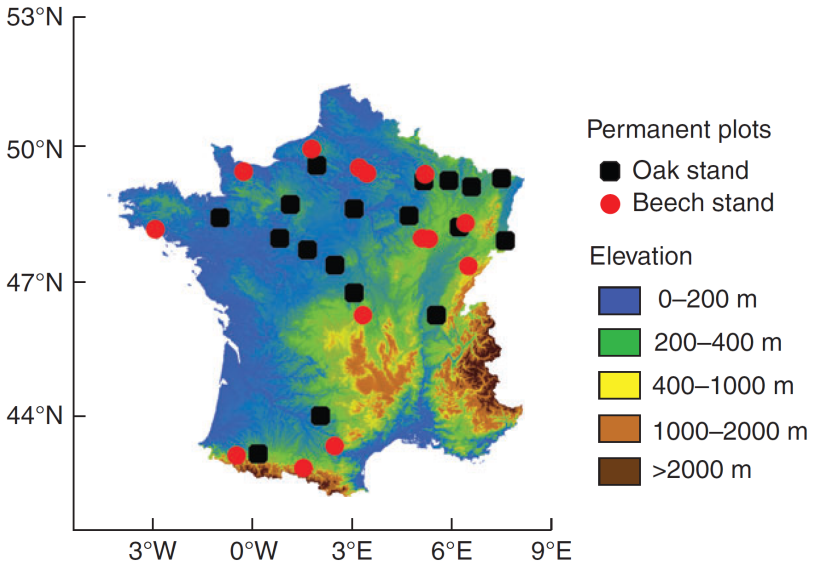

Figure 2: Location and altitude of the RENECOFOR plots.

Plots were set up in even-aged mature forest stands. Growth measurements consisted of (1) dendrochronological sampling: in 1995, 30 overstorey trees per plots were cored to the pith at breast height with an incremental borer (Lebourgeois, 1997). The tree CBHs were also measured. Dendrochronological series were processed with standard methods, tree ring width was precisely measured and the series were dated (Lebourgeois et al., 2005; Mérian et al., 2011). (2) Forest inventories: from 1991 to 2009, extensive CBH surveys were regularly conducted on 0.5 ha in the central part of the plots (Cluzeau et al., 1998), for which thinning events (typically occurring every 8 years) were reported. In a few cases (approx. 15%), unreported thinning could strongly modify the dendrometric characteristics of the plots between two surveys; for this reason, we discarded survey findings displaying a stem number decrease, 2% per year. The dataset finally included 2-5 surveys per plots (Supplementary Data Table S6), with time intervals between two measurements ranging from 2 to 5 years. Other reported site characteristics were site index (calculated from dominant height measurements (Skovsgaard and Vanclay, 2008; Supplementary Data Table S6), soil water holding capacity, LAI_{max} and leaf nitrogen content (LNC). Soil water holding capacity was estimated from soil depth and texture measured on two soil pits per plot (Brêthes and Ulrich, 1997). LAI_{max} was estimated from litter collection (Pasquet, 2002), and sunlit LNC was determined annually on eight trees from 1993 to 1997, using the Dumas method (Croisé et al., 1999). A description of the site characteristics is provided in Supplementary Data Table S6.

2.5 Size-asymmetry of growth

Basal area increments (BAIs) were derived yearly from the tree ring series, assuming a circular cross-section of the trunks. Past CBH trajectories of the cored trees were inferred from the tree ring series and measured CBH, after accounting for changes in bark thickness (Dhôte and Hatsch, 2000). The annual size asymmetry of the growth (i.e. the ability of larger trees to have a higher growth rate than smaller trees) was then evaluated from 1995 backward, using the slope (hereafter γ_{data}) of a simple linear regression fitted to the 30 calculated CBH_j and their corresponding BAI_j . This relationship has been reported to be positive and linear in beech and oak overstorey trees grown in even-aged high stands (Dhôte, 1999; Deleuze et al., 2004; Supplementary Data Fig. S8A, B), with non-zero BAIs above a positive CBH threshold (here after σ_{data}). We investigated the species-specific dependencies of γ_{data} and σ_{data} using both productivity and stand structure variables within the linear mixed model framework. The intraplot correlation among observations was considered by including a temporal covariance structure in the residuals, using a first-order autoregressive model [eqn (9)]. The autocorrelation parameter (ρ) was estimated jointly with the other parameters. The spatial and temporal variability of γ_{data} and σ_{data} were addressed by conducting analyses on both raw data and within-plot standardized data. The terms included in the final model were as follows:

- Species (k, unitless, a factor)
- Site index (SI, m, a covariate): used as a proxy for the site productivities
- Annual productivity (AP, mm^2, a covariate): defined as the annual mean BAI of the cored trees, used as a proxy for the interannual variation of the productivity within a given site
- Maximum CBH (CBH_{max}, cm, a covariate): defined as the mean CBH of the five largest sampled trees, used as a proxy for the dendrometric features of the stands
- γ_{data} or σ_{data} ($mm^2.cm^{-1}$ or cm, respectively, covariates): used to test the significance of the dependency between the two stand structure variables

Overall models could be written as follows:

$$\left\{\begin{array}{l}\gamma_{\text{data}i,j,k} = a + \alpha_k + (b + b_k)\sigma_{\text{data}i,j} + (c + c_k)\text{SI}_j \\ \qquad\qquad +(d + d_k)\text{AP}_{i,j} + (e + e_k)\,\text{CBH}_{\text{max}\,i,j} + E_{i,j,k} \\ \sigma_{\text{data}i,j,k} = a + \alpha_k + b + b_k)\gamma_{\text{data}_{i,j}} + (c + c_k)\text{SI}_j \\ \qquad\qquad +(d + d_k)\text{AP}_{i,j} + (e + e_k)\text{CBH}_{\text{max}i,j} + E_{i,j,k}\end{array}\right\} \tag{8}$$

where i, j and k are year, plot and species, respectively. $\text{Var}(\text{E}_{\text{i, j, k}}) = \sigma^2_{\text{E}}$ was the residual variance, the temporal structure of the residuals being:

$$\text{corr}(E_{i,j,k}, E_{i',j',k'}) = \left(\begin{array}{ll}\rho^{|i-i'|}, & \text{if } j = j' \text{ and } k = k' \\ 0, & \text{otherwise}\end{array}\right) \tag{9}$$

The uncertainty in the γ_{data} and σ_{data} estimations varied strongly among years (Supplementary Data Fig. S8C, D). This uncertainty was considered in the analysis using a bootstrap procedure (Chernick, 2011). Models (8) were fitted 1000 times, randomly sampling at each iteration γ_{data} and σ_{data} values within their 95% confidence intervals. Only parameters with estimate distributions excluding zero values in a bilateral 5% probability level were retained. Analyses were conducted with the lme function of the package nlme in the R software (R Development Core Team, 2013).

2.6 Model parameterization

The PBM CASTANEA includes site-specific parameters (Supplementary Data Table S6) and an important number of species-specific parameters (Le Maire et al., 2005; Davi et al., 2005; Dufrêne et al., 2005; see CASTANEA : species-specific parametrization in the Supplementary Data). The parameters of the SSM are provided in Table 1. In particular, parameterization of the individual tree growth model [eqn (1)] has been based on the analysis of the growth size asymmetry over the RENECOFOR network. Indeed, eqn (1) and the growth size asymmetry analysis both relied on the same relationship between tree CBH and tree BAI (see Size asymmetry of growth section and Fig. 1). For this reason, σ_{sim} and γ_{sim} were parameterized based on σ_{data} and γ_{data} dependencies, respectively.

2.7 Model evaluation

The fully coupled CASTANEA-SSM model was evaluated against forest inventories over the period from 1991 to 2009 (this dataset was not used in the model calibration; see Model structure sections). Forest inventories conducted in 1991 were used to initialize (1) stand biomass in CASTANEA and (2) tree size distribution in the SSM. LAI_{max} was initialized with the averaged value obtained from the litter collection. The SAFRAN database (Vidal et al., 2010) was used for half-hourly climatic forcing. The simulations also benefited from site-specific field measurements of leaf nitrogen content and soil water-holding capacity. We assessed the ability of CASTANEA-SSM to simulate the averaged basal area increment and the averaged mean CBH increment of beech and oak stands grown under contrasted conditions. The moderate Pearson correlations between these two observed variables (r = 0.58 and r = 0.51 for beech and oak, respectively) indicate that they provide complementary information on stand structure changes. Model performance was evaluated using the coefficient of determination of the model (R^2), root mean square error (RMSE) and average bias (AB) (Vanclay and Skovsgaard, 1997).

Treatment	Description	$RDI_{initial}$	RDI_{final}	$N_{initial}$	N_{final}
C	Natural self-thinning (control)	1	1	590	450
T1	Commercial thinning: low intensity	0·9	0·7	590	90
T2	Commercial thinning: intermediate intensity	0·9	0·55	590	60
T3	Commercial thinning: high intensity	0·7	0·4	590	45

Table 2: $RDI_{initial}$ and $N_{initial}$ are RDI and stem number per hectare at the beginning of the simulation (age = 40); RDI_{final} and N_{final} are RDI and stem number per hectare at the end of the forest rotation (age = 150). N_{final} are approximate values.

2.8 Assessing management effect on forest functioning at the France scale

We run CASTANEA-SSM over metropolitan France with an 8 km resolution, using the SAFRAN grid for climate inputs (1989-2009 period, looped six times) and soil parameters from the French soil database aggregated to 8 km resolution to provide spatialized soil water-holding capacity (Cheaib et al., 2012, Supplementary Data Fig. S2). All grid points were initialized with a given tree size inventory and leaf nitrogen content and run over 110 years (stand ageing from 40 to 150 years) and 70 years (stands ageing from 40 to 110 years) for oak and beech, respectively. The

initial CBH inventories for this simulation exercise were obtained from the youngest available stands: HET25 for beech (41 years) and CHP65 for oak (54 years). We ensured therefore to initialize CASTANEA-SSM with realistic CBH distributions. Thinning events were then shared among tree with a thinning strategy from below . The thinning strategy index T_{strat} was set to 1, corresponding to a preferential cutting of small trees, with the probability of cutting declining linearly with CBH (Bellassen et al., 2010). Four simulations were run with contrasted parameterization of the SSM (Table 2), corresponding to contrasted thinning intensities: a control treatment (C) and three treatments of increasing thinning intensity (T1-T3). The highest thinning intensity goes beyond the current guidelines (approx. 70 stems are currently recommended at the end of the forest rotation; Bock et al., 2007; Sardin, 2008). We assessed the influence of thinning on C fluxes [gross primary productivity (GPP), total autotrophic respiration (R_{tot}) and net primary productivity (NPP)] and growth [above-ground biomass increment (AGBI)] averaged over the forest rotation. We additionally analysed the distribution of average AGBI values over the territory. We restricted our analysis to the grid cells where the species presence had effectively been observed (IFN, France, http://inventaire-forestier.ign.fr/spip/) and where CASTANEA predicted no partial or complete mortality event (i.e. not at the species distribution margins, representing >90% of the IFN grid cells): 2951 and 5403 grid cells were retained for beech and oak, respectively.

3 Results

3.1 Variation of the mode of competition

We observed a significant positive correlation between the size-asymmetry index γ_{data} and productivity for both species (Supplementary Data Table S7): (1) across stands, with γ_{data} being greater on sites with high productivity (estimated through the site index, Fig. 3A, C); and (2) within stands, temporal variations of γ_{data} were linked to the interannual variability of productivity (Fig. 4A, B). Slopes of the γ_{data} productivity relationship differed significantly between oak and beech at both scales (Supplementary Data Table S7). On the other hand, the circumference (CBH) threshold for significant growth σ_{data} was found to be only related to the maximum CBH of cored trees (CBH_{max}), with non-different slopes across species at both spatial (Fig. 3B, D) and temporal (Supplementary Data Fig. S7A, B) scales. There was no significant

dependency between σ_{data} and γ_{data} (Supplementary Data Table S7).

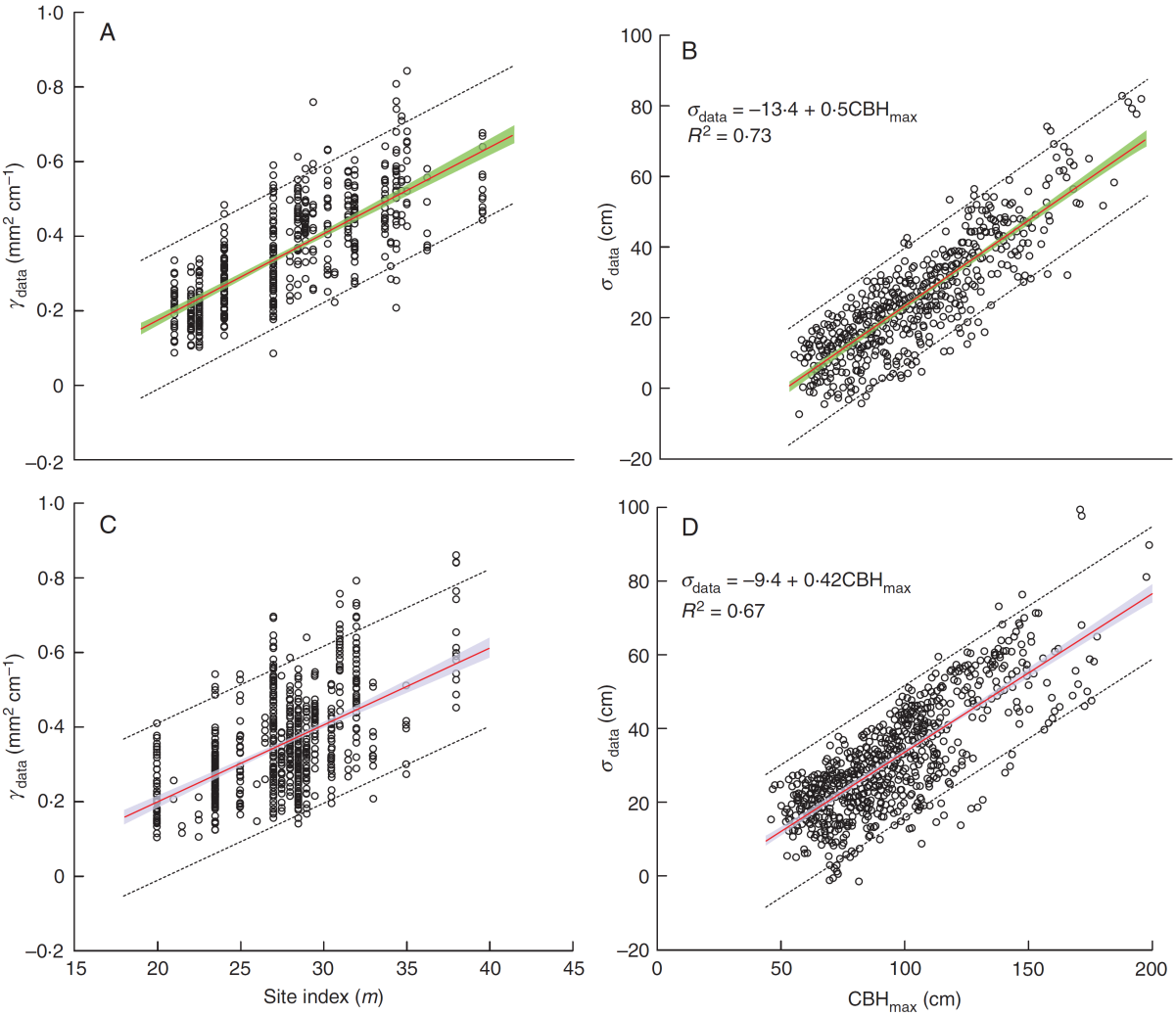

Figure 3: Significant dependencies of γ_{data} and σ_{data} at the spatial scale for beech (A, B) and oak (C, D). Red lines are regression fits, dotted lines are 95% prediction intervals, coloured areas are 95% confidence intervals for beech (green) and oak (blue)

3.2 Modelling of the changes in stand structure

The SSM parameterization aimed at reproducing the spatial and temporal dynamic of the mode of competition, which determines the evolution of the stand structure. Consequently, σ_{sim} was first calculated using the σ_{data} - CBH$_{\text{max}}$ dependency (Fig. 3B, D). The γ_{sim} value was then adjusted so that the sum of the tree volume increments matched the CASTANEA stand-level prediction. High stand-level productivity thus meant more size-asymmetric simulated growth.

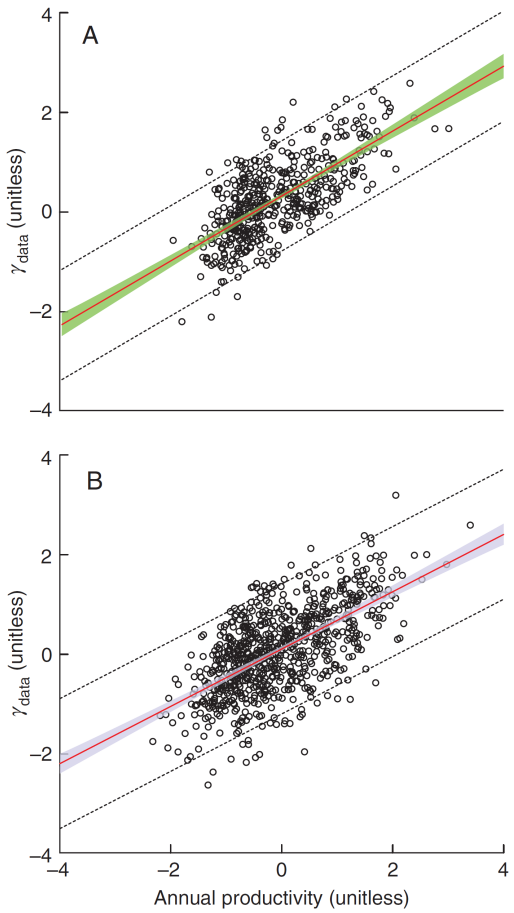

Figure 4: Significant dependency of γ_{data} at a within-plot, temporal scale (within-plot standardized data, unitless) for beech (A) and oak (B). Red lines are regression fits, dotted lines are 95% prediction intervals, coloured areas are 95% confidence intervals for beech (green) and oak (blue).

3.3 Performance of the fully coupled CASTANEA-SSM model

As a prerequisite result, CASTANEA calibrated over the 1970-1990 period was able to simulate the averaged stand volume increments ($R^2 = 0.79$ and $R^2 = 0.87$ for beech and oak, respectively; data not shown). Further, the fully coupled CASTANEA-SSM efficiently predicted the changes in average temporal stand structure from 1991 to 2009, assessed through stand basal area (Fig.5A, C) and mean stand CBH (Fig.5B, D) increments, with $R^2 > 0.8$. CASTANEA-SSM predicted well the structure changes of stands with contrasted productivities, reflecting a large panel of environmental conditions (Fig. 5). No significant average bias was found in the prediction of both variables (i.e. the 1:1 line of a given plot is included in the 95% confidence interval of the fitted regression line).

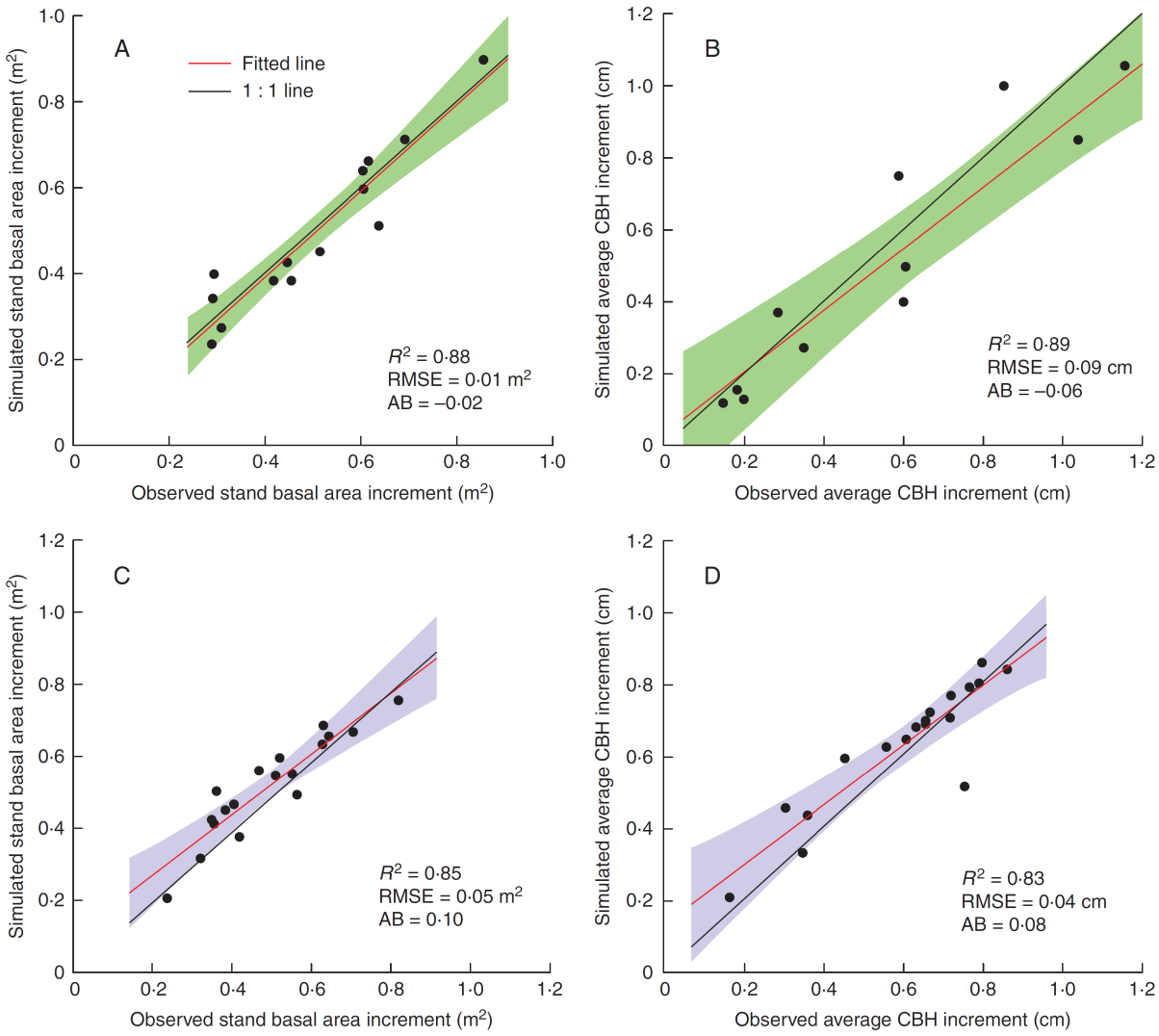

Figure 5: Evaluation of the fully coupled CASTANEA-SSM on long-term stand structure datafrom forest inventories, for beech (A, B) and oak (C, D). Coloured areas are the 95% confidence interval of the fitted regression lines for beech (green) and oak (blue). AB, average bias; RMSE, root mean square error.

3.4 Simulated management effect on growth at the national scale

Increasing intensity of thinning had a quasi-linear effect on the averaged stand atmosphere C fluxes and on growth for both species (Fig. 6). Thinning had a very slight negative effect on GPP, even in the case of heavy thinning (Figs 6A and 8), but the effect on R_{tot} was consistently negative (Fig. 6B). Consequently, increasing intensity of thinning resulted in a significant increase in NPP (Fig. 6B). This additional quantity of C fixed within the stand is then distributed among the different compartments according to the allocation rules of CASTANEA, which led to a slight increase in the AGBI (Fig. 6C). This increase in AGBI was low and comparable between beech

and oak (approx. 7 $gC.m^{-2}.year^{-1}$; Fig. 6C). We observed that thinning changed the average C allocation to the CASTANEA compartments: above-ground biomass increment increased by approx. 3% in the heavy thinning treatment (T3) compared with the control (Supplementary Data Fig. S9), while fine root biomass and carbohydrate reserve increments increased by approx. 20 and 11%, respectively (Supplementary Data Fig. S9).

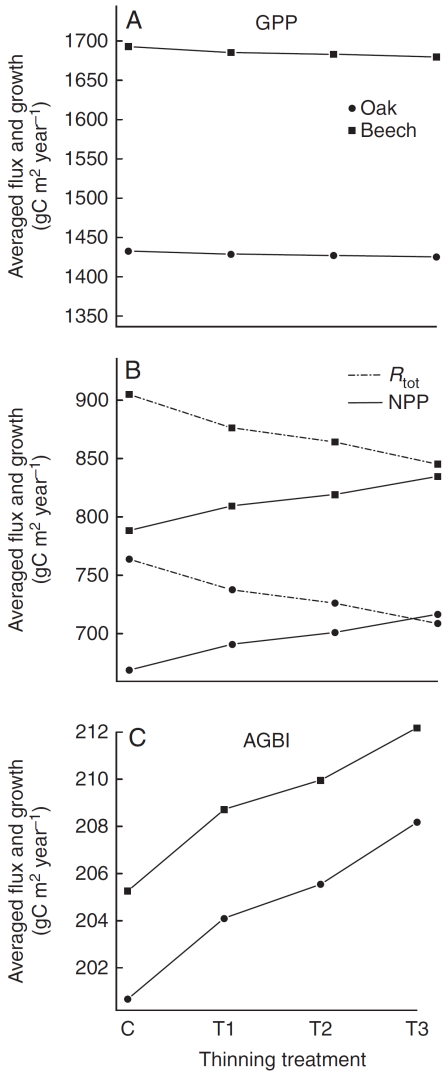

Figure 6: Effect of contrasted thinning treatments on average fluxes and growth over France for beech and oak (as indicated in the key).(A) Gross primary productivity (GPP), (B) net primary productivity (NPP) and total autotrophic respiration (R_{tot}), (C) above-ground biomass increment (AGBI).Thinning treatments: C, control; T1-T3, treatments with increasing thinning intensities.

Because the simulated impact of thinning on forest functioning appeared to be consistent, we only drew a comparison between C and T3 (the highest thinning intensity) treatments in the following analysis. The AGBI distribution of both species revealed that heavy thinning had a contrasted (0-8 and 2-6% for beech and oak, respectively) effect on growth over France

(Fig. 7A, B). The maximum relative growth increase was reached in cells with moderate fertility, corresponding to the intermediate growth rate in the control treatment.The dispersion of the relative influence of thinning on growth also reached a maximum in moderate fertility zones, and was higher for oak stands (Fig. 7A, B). The highest increases in relative growth were observed for cells where thinning induced an important decrease in average LAI_{max} over the forest rotation (Supplementary Data Fig. S10). The thinning-induced effect on LAI_{max} was related to the frequency and the intensity of the silvicultural operations (Fig. 8), but also to average annual water stress (Supplementary Data Fig. S11), which determine the LAI_{max} post-thinning resilience (i.e. the time needed to recover initial LAI_{max}, Fig. 8). The thinning-induced drop in average LAI_{max} was strongly related to an alleviation of water stress over the forest rotation (Supplementary Data Fig. S11). Overall, the grid cells could be pooled in three distinct categories (Fig. 7), as follows.

- Cells with a moderate thinning effect (<4%) and high growth(>180 gC m^{-2}.$year^{-1}$). These cells where characterized by optimal conditions for growth, especially low water stress. Consequently LAI_{max} recovered quickly after cutting (Fig. 8) and the thinning effect on growth was moderate.

- Cells with a moderate thinning effect (<4%) and low growth (<180 gC.m^{-2}.$year^{-1}$). In these cells, little thinning occurred (Fig. 8) because growth was strongly limited by different environmental factors (e.g. high water stress, low temperature or low radiation, which limit photosynthesis and growth). Thinning-induced effects on growth were thus limited. This group also includes cells where LAI_{max} decreased in response to a lack of carbohydrate reserves, reducing the relative impact of thinning.

- Cells with a high thinning effect(>4%). In these cells, growth was high enough to trigger a regular thinning (due to a rapid RDI increase; Supplementary Data Fig.S1). The thinning effect on LAI_{max} was important because of medium to high annual water stress, leading to low post-thinning resilience (Fig. 8).

Areas displaying a moderate influence of thinning are consequently primarily located at high elevation or at the southern edge of the species distribution (group2; 20 and 14% of the territory for beech and oak, respectively), and in high forest productivity zones in northern and eastern France (group 1; 56 and 59% of the territory for beech and oak, respectively). Areas where the

thinning effect was high (group 3; 24 and 27% of the territory for beech and oak, respectively) are located a low elevation plains (Fig. 2) where annual water stress is high (Fig.7) because of high climatic water demand or low soil water-holding capacity (Supplementary Data Fig. S2).

4 Discussion

We present a new functional structural model allowing prediction of stand structure changes over forest rotation. Our model is built upon the coupling between the physiological knowledge provided by the CASTANEA model and an SSM based on an empirical relationship between individual tree size and growth. CASTANEA-SSM was successfully evaluated against averaged dendrometric variables from inventories of 20 years in deciduous forests throughout France. The ability of the model to reproduce the temporal evolution of the entire tree size distribution characteristics (e.g. size inequality and skewness) could not be evaluated in this restricted time period survey. However CASTANEA-SSM satisfactorily simulates the changes in general features expected in a tree size distribution across a temperate forest rotation (i.e. simulated coefficient of variation and skewness decrease with stand mean size; data not shown). The coupled CASTANEA-SSM model can be used to explore the effect of realistic and operational thinning strategies on stand functions, by simulating stand variables usually found in forest management (e.g. RDI, basal area). Further, the coupled model allows simulation of adaptive silviculture, with a thinning frequency function of the individual growth rate, in order to investigate the impact of climate change on wood supplies (Pussinen et al., 2009). Lastly, CASTANEA-SSM will be used to investigate the impact of fundamental competition rules (such as self-thinning; Caspersen et al., 2011) on long-term forest stand functioning, along with the size dependency of physiological processes (e.g. the effect of hydraulic conductance on stomatal control and growth), which has been reported as a major key challenge for physiological modelling (Poschenrieder et al., 2013). In the following we discuss: (1) the rules of tree growth competition used in the SSM calibration; (2) the functional implications of thinning in terms of stand atmosphere C fluxes and within-stand C allocation; and (3) the potential of management to affect forest functioning at the national scale.

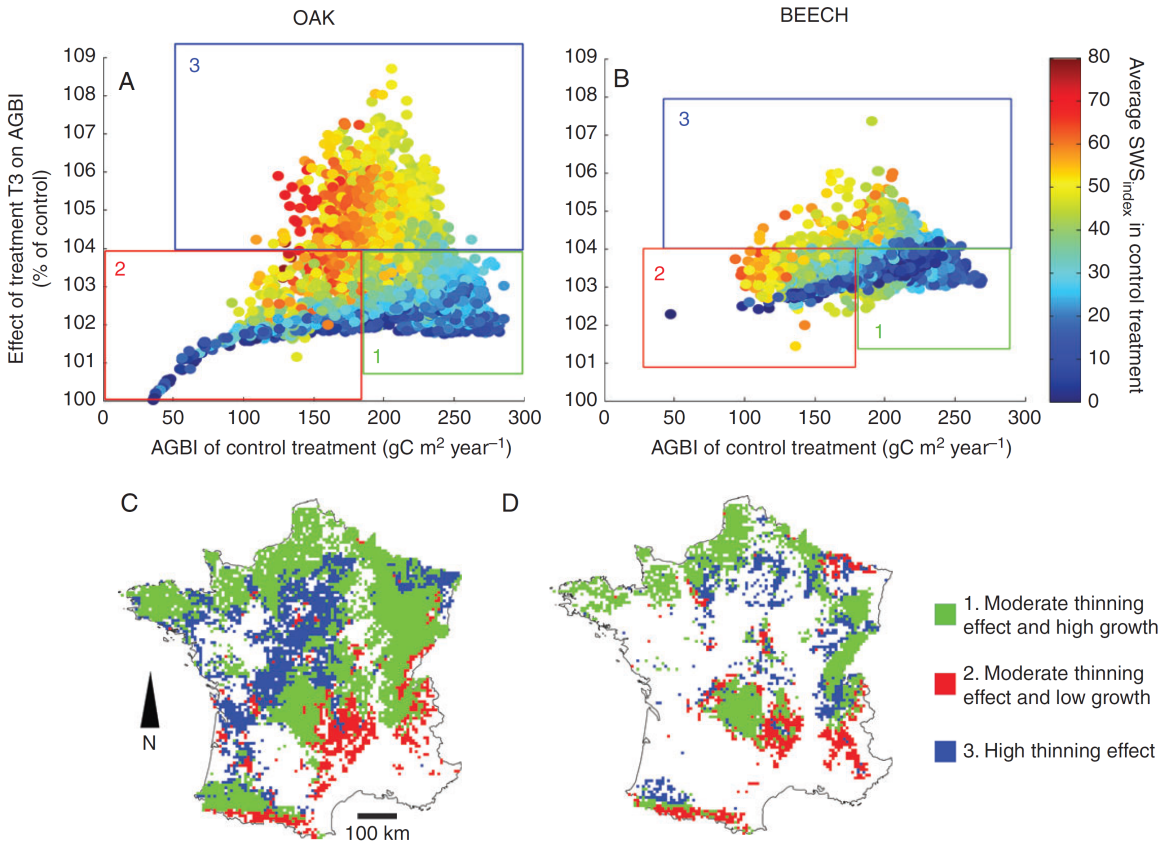

Figure 7: Effect of thinning treatment (T3) on AGBI over France (averaged over a forest rotation): relationship to the average absolute AGBI and SWS_{index} in the control (A, B) and location of the grouped grid cells (C, D). Groups 1-3 defined in (A) are mapped in (C) (oak); groups 1-3 defined in (B) are mapped in (D) (beech).

4.1 The rules of tree growth competition in beech and oak temperate forest

The SSM is based on the widely acknowledged relationship between tree size and growth (Coomes et al., 2011). Size growth relationship prediction indeed allows determination of the changes over time of an initial tree size distribution and is therefore related to changes in size inequality and stand structure. The annual size growth relationship was assumed to be a simple regression line between tree circumference (CBH) and tree basal area increment (BAI). The two parameters of the size growth relationship, namely the slope and the circumference threshold for significant growth, provided complementary information on tree competition rules.

On the one hand, we found a positive and significant relationship between the size asymmetry of growth (assessed through the slope parameter γ_{data}) and the stand productivity at both temporal and spatial scales and for both species (Figs 3 and 4). This result is in line with the findings of Pretzsch and Biber (2010) and Pretzsch and Dieler (2010), and confirms that increasing

fertility, related either to among-site differences or to interannual climatic variations, induces a transition in the competition among trees from size symmetric to size asymmetric. This finding is consistent with the premise that under favourable growth conditions, the disproportional advantage of large trees in the competition for light leads to size asymmetry of growth. Conversely, under adverse conditions (i.e. under water or nutrient limitations of growth), competition is thought to be more size symmetric. We additionally reported that growth size asymmetry increased more rapidly with productivity for beech than for oak at both temporal and spatial scales. Beech is indeed more shade tolerant than oak (VonLüpke, 1998), meaning that small beech trees can grow and survive in the stand understorey. Consequently, the canopy structures of beech stands are expected to be more heterogeneous, leading to more size-related competition for light when below-ground resources are not limiting. However, we must acknowledge that using growth as a proxy for competition-mediated resource distribution can be misleading (Weiner and Damgaard, 2006), for instance in the case of a strong size effect on the resource use efficiency. On the other hand, we found no dependencies between productivity and the CBH threshold (parameter σ_{data} , Supplementary Data Table S7). A shift in this threshold corresponds to an equal BAI fluctuation in all the growing trees; for this reason, this result indicates that there was no higher sensitivity of smaller trees to the variability of the growth conditions. This finding is in line with the conclusions of Mérian and Lebourgeois (2011) and contradicts evidence that smaller trees experience greater water stress because of greater below-ground competition in beech and oak temperate forests (Jacquart et al., 1992; Kloeppel et al., 1993; see also De Luis et al., 2009 for Pinus sp.). Rather, we found that the CBH threshold σ_{data} was significantly related to the CBH of the largest sampled trees at both temporal and spatial scales, with a similar slope for beech and oak (Fig. 3; Supplementary Data Table S7). This dependency could be due to the shift toward higher CBH of the growing tree distribution as the stand ages: CBH trajectories of the smallest trees with non-zero growth are strongly correlated with those of the largest trees in even-aged beech and oak stands (Dhôte, 1999). We consequently highlighted a monotonous change with stand age of the CBH threshold for significant growth, which is not influenced by the environmental factors causing growth to vary and indicates a conservative size hierarchy in beech and oak stands. Further, these results indicate that tree growth competition in deciduous mature temperate forest can be represented without the spatially explicit framework that strongly limits the potential applications of most tree-level growth models (Poschenrieder et al., 2013).

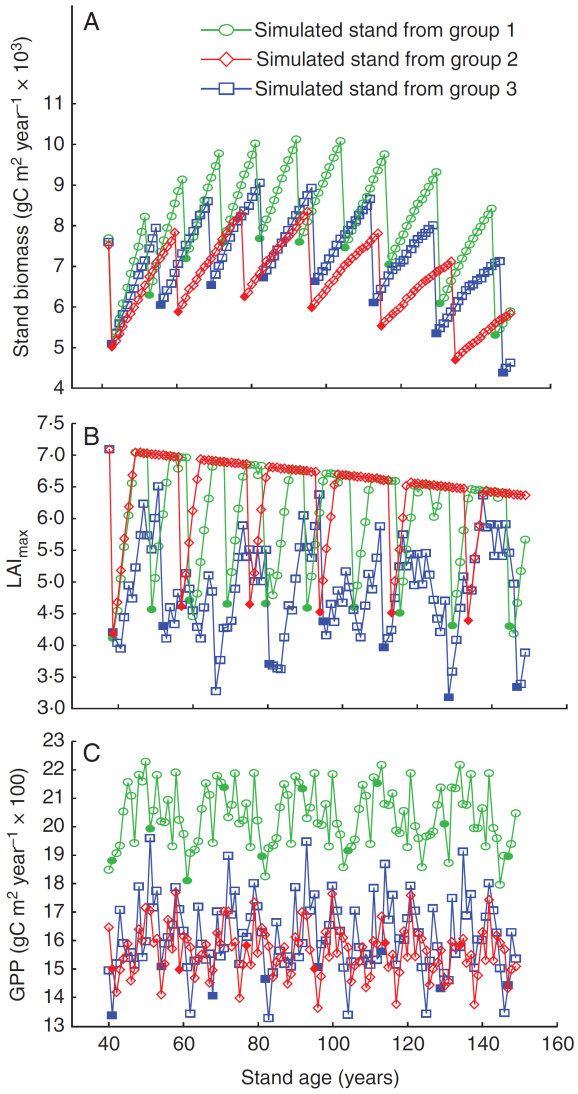

Figure 8: Simulated temporal dynamics of stand biomass (A), LAI$_{max}$ (B) and gross primary productivity (C) over a forest rotation for oak stands. Filled symbols indicate year of thinning.

4.2 The functional implications of thinning

A coupled process-based empirical modelling of the size-growth relationship fluctuations successfully reproduced the effects of environmental factors and tree-to-tree competition on average stand structure changes across a wide ecological gradient. We were consequently able to quantify the influence of thinning on forest C fluxes and growth over France, to highlight the potential of management to affect forest functioning. We compared the effects of contrasted management regimes: a control treatment where only self-thinning occurs and three contrasted thinning intensity treatments. Increasing thinning intensity led to an increase in NPP which was the result of two different effects of thinning (Fig. 6), a slight decrease in GPP and a stronger decrease in

R_{tot}. The important negative thinning effect on R_{tot} is tightly linked to the reduction of the living stand biomass. This is realistic as the maintenance respiration of the above-ground woody biomass (stem and branches) represents about one-third of the total C lost by the ecosystem in a beech forest (Granier et al., 2000; Damesin et al., 2002). Moreover, CASTANEA is able to reproduce this proportion of ecosystem C losses efficiently (Davi et al., 2005). Conversely, the reduction in annual LAI_{max} following thinning had little average impact on GPP whatever the thinning intensity (Figs 6 and 8). This result, in line with the report from Grote et al. (2011), is primarily due to the asymptotic relationship between LAI_{max} and GPP (LeMaire, 2005), which is a direct consequence of both the exponential decrease of visible light interception (Monsi and Saeki, 2005) and photosynthetic capacity (Ellsworth and Reich, 1993) in the canopy.

Further, we observed that thinning-induced LAI_{max} reduction could significantly alleviate the average stand water stress (maximum approx. 10%; Supplementary Data Fig. S11) by reducing canopy transpiration. The incident global radiation, strongly linked to the canopy transpiration (Monteith, 1981), is indeed moderately attenuated when going from the top to the bottom of the canopy (Baldocchi et al., 1984). As a consequence, transpiration occurs in all the canopy layers and a decrease in LAI_{max} leads to a decrease in canopy transpiration even if the LAI_{max} remains at high values ($LAI_{max} > 4$; Fig. 8). This thinning-induced water stress alleviation has positive effects on stomatal conductance and C assimilation, and is therefore another factor reducing the detrimental effect of canopy reduction on GPP. In line with these results, LAI reduction has been shown to be an important process in the long-term forest acclimation to drought (Martin-StPaul et al., 2013). A positive effect of thinning on stand water relations has been assessed for a long time in field experiment (e.g. Bréda et al., 1995; Rodriguez-Calcerrada et al., 2011) but still had to be incorporated within stand growth PBMs to quantify the intensity and duration of thinning effects on fundamental processes and define future adaptive guideline. On first exposure, the positive effect of thinning on NPP and AGBI conflicts with an empirical rule widely use in forest sciences: the so-called Eichhorn rule states that thinning does not significantly influence stand growth for a wide range of silvicultural intensities (Skovsgaard and Vanclay, 2008). However, this statement has to be discussed considering (1) the debate about the generality of the Eichhorn rule; (2) the limitation of our modelling approach; and (3) the low amplitude of the thinning-induced effect on growth and its functional causes. Indeed, one should note that the generality of the Eichhorn rule is still under debate; other

relationships are suggested that imply an optimal thinning intensity for stand growth, in line with our results (Zeide, 2001; Skovsgaard and Vanclay, 2008). On the other hand, the limits of our modelling approach have to be considered. The simulated canopy of the CASTANEA PBM cannot be used to predict the functioning of open-grown trees, so we restricted our analysis to closed-canopy silvicultural guidelines (around 45 stems at the end of a forest rotation in the T3 treatment). This can explain that we did not report an important GPP drop when simulating heavy thinning treatment. Besides, CASTANEA-SSM did not include allometric scaling laws that could have resulted from natural selection-driven vascular network optimality: under this hypothesis, vascular networks minimize hydrodynamic resistance while maximizing resource uptake, which set allometric constraints in plant development (Enquist, 2002). These allometric constraints could put a physical limit on the potential growth of trees and thus on the stand growth capacity under low stem number heavy thinning treatment (the maximum simulated CBH at the end of the forest rotation was approx. 3.5 m in our modelling exercise). Most importantly, we observed that the amplitude of growth change was weak, especially compared with biomass estimation uncertainty (Lecointe et al., 2006), which makes it difficult to assess in the field. A major reason for this low absolute effect of thinning is the changes in average C allocation. Our simulations revealed that the extra C assimilated after thinning is predominantly attributed to the fine root compartment (Supplementary Data Fig. S9), following allocation equilibrium rules between leaf, fine root and carbohydrate reserve implemented in CASTANEA (Davi et al., 2009). The maintenance respiration C cost of fine roots is high (Ryan et al., 1996; Epron et al., 1999) and consequently limits the decrease of total respiration - and the associated increase in NPP and AGBI - following stand woody biomass reduction. This finding is in line with field experiments reporting enhanced biomass and turnover of fine roots after thinning (Santantonio and Santantonio, 1987; Lopez et al., 2003). Our modelling approach thus suggests that changes in C allocation are a plausible physiology-based explanation of the empirical Eichhorn rule.

4.3 The potential of management to affect forest functioning at the national scale

Our simulations clearly indicated an enhancement of net C assimilation and growth in managed forests. This positive thinning effect appeared to be different over the territory for the two species. We showed that the intensity and frequency of thinning strongly interact with LAI_{max} resilience

in determining the thinning effect on growth (Fig. 8). The management effects appear to be more contrasted over France for the oak stand (Fig. 7), mainly because LAI_{max} resilience is lower and thinning therefore has a longer effect on forest functioning (see CASTANEA: inter-annual variation of LAI_{max} in the Supplementary Data). Under the hypothesis of forest management for commercial purposes, the intensity and frequency of thinning are determined by the forest productivity: the higher the growth, the more frequently silvicultural operations are required to keep the stand within the guideline boundaries. This partially explains the low thinning effect on low growth stands, so this result could be different, for example, in the case of high thinning intensity to maintain relict stands at the edge of the species distribution (Perez-de-Lis et al., 2011). The highest thinning effect was reached in a zone with regular thinning interventions and low LAI_{max} resilience due to moderate to high water stress (corresponding to forest with current intermediate productivity). Interestingly, these zones will be the first production forests impacted by the increase of drought intensity and frequency mediated by climate change.

4.4 Conclusions

Our modelling approach consequently could help in identifying the proportion of the territory where management efforts should be concentrated to mitigate near-future drought impact on national forest productivity. Around a quarter of the French temperate oak and beech forests are currently in zones of high management potential and high climate change vulnerability. This proportion could increase rapidly if increasing water stress affects non-limited high growth stands. Process-based models incorporating stand structure modelling can be used to define physiology-based adaptive management prescriptions (Pussinen et al., 2009): our findings indicate that heavy thinning beyond the current guidelines (approx. 50 stems at the end of the forest rotation) could profitably be tested without productivity loss.

5 Supplementary data

5.1 Simulated features over forest rotation of a stand under thinning treatment

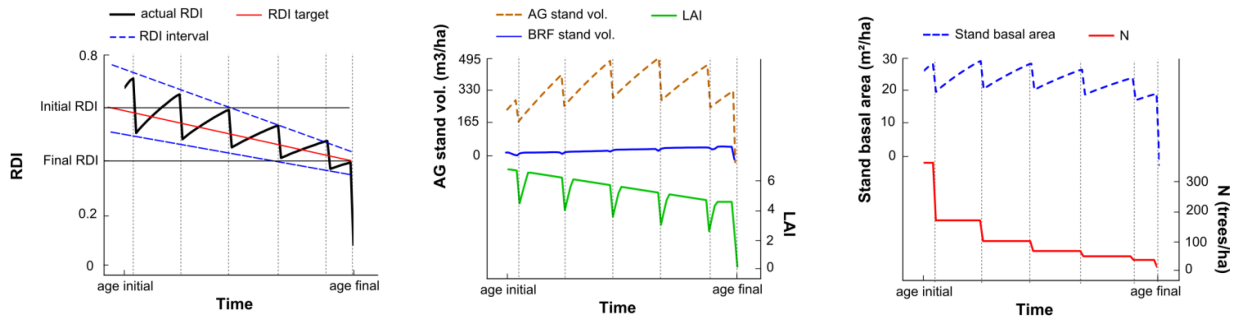

Figure S1: Simulated features over forest rotation of a stand under thinning treatment. Abbreviations: RDI (relative density index), LAI_{max} (annual maximum leaf area), N (stand stem number), AG (above ground), FRB (fine root biomass), vol. (volume).

5.2 Spatialized soil parameter

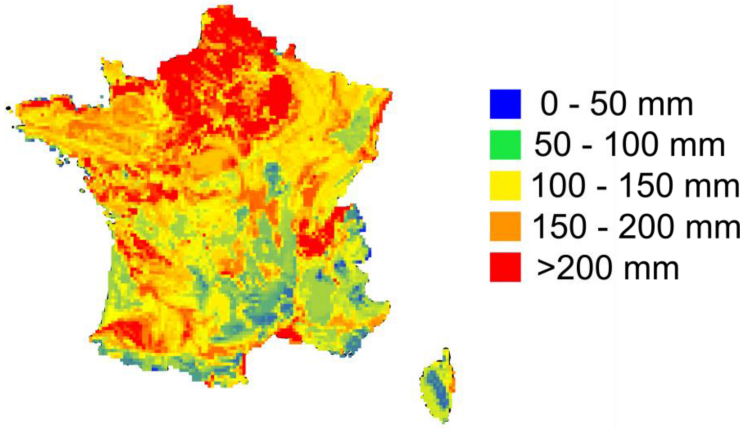

Figure S2: Soil water holding capacity over France (Cheaib et al. 2012).

5.3 Above ground volume calculation

The same procedure has been used for the calculation of observed and predicted stand volumes from CBH distribution.

5.3.1 Top height

Following Le Moguédec and Dhôte (2011), we used for oak the top height curves established by Duplat and Tran-Ha (1997):

$$H_0 = m_1 + (m_2 A + m_3 H_{100} + m_4)\left[1 - e^{-m_5 . A^{m_6}}\right]^{m_7} + (m_8 + m_9 H_{100}).A \quad \text{(S1)}$$

where,

- H_0 is the top height of the stand (m)
- A is the age of the stand (m)
- H_{100} is the site index (m)

For beech, a Lundqvist-Matérn equation established by Bontemps (2006) was used:

$$H_0(A) = K.e^{-\left[\left(ln\frac{K}{H_{A_0}}\right)^{-m} + \frac{R.m.C_m}{K}(A - A_0)\right]^{-\frac{1}{m}}} \quad \text{(S2)}$$

with

$$C_m = e^{(1+m)[1-\ln(1+m)]} \quad \text{(S3)}$$

where,

- A_0 is a reference age
- $H_{(A_0)}$ is the stand top height at the age of A_0

Parameterization of eq. (S1), (S2) and (S3) is provided in Table S1.

Species		Parameter values
Oak		m_1=0.3; m_2=-0.039339; m_3=0.78595; m_4=-7.10703; m_5=0.0024168; m_6=1.56; m_7=0.7119; m_8=0.10445; m_9=0.00235
Beech	Western France	A0=5; H_{A0}=1.3; K=44; R=0.4; m=0.517
	Eastern France	A0=5; H_{A0}=1.3; K=67.3; R=0.4; m=1.218

Table S1: Parameterization of the top height curves.

5.3.2 Individual height

The height of each tree is then calculated using the hyperbolic model suggested by Dhôte and de Hercé (1994):

$$H = 1.3 + \frac{((H_0 - 1.3 + p_2.CBH) - \sqrt{H_0 - 1.3 + p_2.CBH)^2 - 4.p_3.p_2.(H_0 - 1.3).CBH}}{2.p_3} \quad \text{(S4)}$$

where H is the height of a given tree with a circumference CBH. p2 and p3 get the values 0.373 and 0.98812 or 0.412 and 0.98764, for oak and beech, respectively.

5.3.3 Individual volume equations

Tree above-ground volumes were calculated from CBH and H, using the equations established by Vallet et al. (2006):

$$V = form \frac{1}{40000\pi} CBH^2.H \quad \text{(S5)}$$

where V is the total above ground tree volume and

$$form = (\alpha + \beta.CBH + \gamma.hdn)(1 + \frac{\delta}{CBH^2}) \quad \text{(S6)}$$

with hdn = $CBH^{1/2}$ / H. Parameterization of eq. (S5) and (S6) is provided in Table S2.

Parameter	Oak	Beech
α	0.471	0.395
β	-0.000345	0.000266
γ	0.377	0.421
δ	0	45.4

Table S2: Parameterization of the tree volume equations.

Individual volume were then summed up and standardized to the area (ha) unit.

5.3.4 Wood density model

CASTANEA predicts annual carbon mass increment (Dufrêne et al. 2005) and SSM input needs annual volume increment, for this reason we additionally needed density estimations to ensure the coupling between the 2 sub-models. The dry matter mass was converted to carbon mass by multiplying by 0.5 (Pignard et al. 2000). Wood density models typically relates the density of a tree ring formed in year i (WD_i) to tree age (age_i) and ring width (RW_i) (Guilley et al. 2004; Bergès et al. 2008). We used density models established by:

- Zhang et al. (1993) for oak, with WD models as

$$WD_i = \frac{a+b.age_i-(\frac{c}{RW_i})-(\frac{d.age_i}{RW_i})}{1.235} \quad \text{(S7)}$$

- Bouriaud et al. (2004) for beech, with

$$WD_i = \frac{a-b.age+\frac{c}{RW_i}}{1.3} \quad \text{(S8)}$$

Parameterization of eq. (S7) and (S8) is provided in Table S3.

Parameter	Oak	Beech
a	817.9	789
b	0.0038	0.86
c	98.927	0.32
d	0.922	-
e	1.235	1.3

Table S3: Parameterization of the tree volume equations.

Annual wood density was calculated for all the available dendrochronological tree ring series (30 trees per RENECOFOR plot). Site-specific averaged values were then retained for the conversion of dry matter to volume. Density values were typically comprised between 560 and 610 g.dm^{-3}, or between 540 and 580 g.dm^{-3} for oak and beech, respectively.

5.4 SSM: Harvest sub-model

In order to determine which trees will die in a mortality event (self-thinning or commercial cutting), a probability of death is attributed to each tree, following Eq. (S9) (Bellassen et al. 2010).

$$\begin{cases} if\ T_{strat} \geq 0: P_i = P_{min} + (P_{max} - P_{min}) \times \left(\frac{CBH_{max} - CBH_i}{CBH_{max} - CBH_{min}}\right)^{T_{strat}} \\ if\ T_{strat} < 0: P_i = P_{min} + (P_{max} - P_{min}) \times \left(\frac{CBH_{max} - CBH_i}{CBH_{max} - CBH_{min}}\right)^{T_{strat}} \end{cases} \quad \text{(S9)}$$

where,

- P_i is the death probability of the tree i
- CBH_i is the CBH of the tree i
- CBH_{min} and CBH_{max} are the minimum and maximum CBH of the tree distribution, respectively
- P_{min} and P_{max} are the minimum and maximum death probability, respectively
- T_{strat} is the thinning strategy index T_{strat} determines the thinning strategy: if $T_{strat} > 0$, smaller trees are preferentially thinned (thinning from below see Pretzsch (1998)) whereas

if $T_{strat} < 0$ (thinning from above) biggest trees get a higher death probability. In case of self-thinning, T_{strat} is set to 0.5.

A score S is finally attributed to each tree, following Eq (S10).

$$S_i = U \times P_i, \quad U \sim U([0,1]) \tag{S10}$$

where S_i is the score of a tree i and U is a realization of a random variable with a uniform probability distribution. Trees with the highest scores are then removed to decrease the stand RDI to the proper value, following the algorithm described in Figure S1.

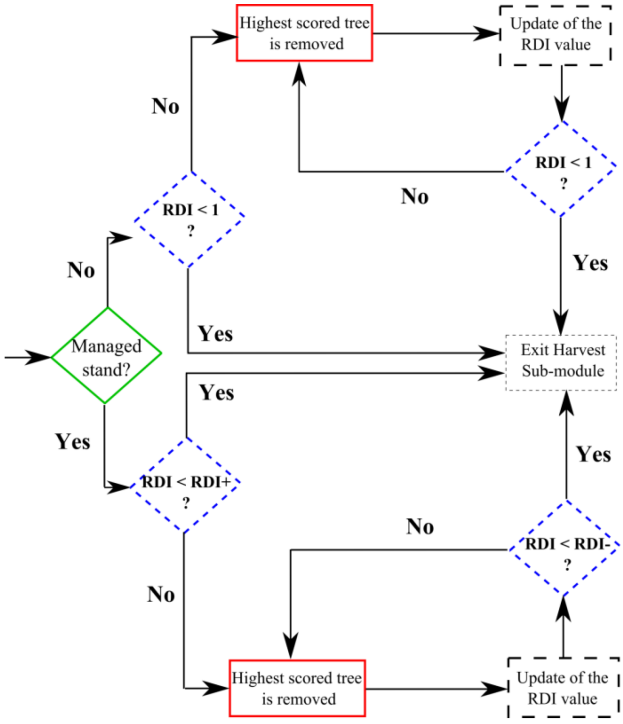

Figure S3: Tree removal algorithm. RDI+ corresponds to RDI_{target}*(1+RDIl), RDI- corresponds to RDI_{target}*(1-RDIl).

5.5 CASTANEA: soil water stress index

The soil water balance model is basically a bucket one with 2 layers (a top soil layer and a total soil layer, including top soil layer) (Dufrêne et al., 2005). Based on the soil water balance, an

index of water stress (reduc, unitless) is calculated daily and aggregated over year.

$$reduc_t = \max(0, \min(1, \frac{SWC_t - SWC_{wilt}}{0.4 \times (SWC_{fc} - SWC_{wilt})})) \quad \text{(S11)}$$

where SWC_t is the soil water content of day t (mm), SWC_{wilt} is the soil water content at wilting point (mm) and SWC_{fc} is the soil water content at field capacity (mm). reduc calculation is based on the water stress effect on stomatal conductance (Granier et al. 1999). In addition,

$$reduc_t = 1 \text{ if } SWCtop_t > SWCtopwilt \quad \text{(S12)}$$

where SWC_{topt} is the soil water content of the top soil layer (mm) and $SWCtop_{wilt}$ is the soil water content of the top soil layer at wilting point (mm). This aims to reproduce the positive effect of light rain (only affecting top soil water balance) on stomatal conductance (Dufrêne et al., 2005). Finally,

$$SWS_{index} = \sum_{t=1}^{365} (1 - reduc_t) \quad \text{(S13)}$$

where SWS_{index} (unitless) is the soil water stress index, an integrated variable of water stress intensity in a given year.

5.6 inter-annual variation of LAI_{max}

This new module has been calibrated on LAI data from the Barbeau forest site (E. Dufrêne, CNRS, France, unpubl. res, http://max2.ese.u-psud.fr/SiteBarbeau/index.html) and 8 plots in the Fontainebleau forest for oak, 7 plots in the Fontainebleau forest for beech (Dufrêne and Bréda 1995; LeDantec et al. 2000). LAI_{max} variation is calculated annually as a function of SWSindex of the previous years (Fig. S4). For beech,

$$deltaLAI_{max}(n) = \max(-1.5, \min(1.5, 1.51 - 0.0263 \times SWS_{index}(n-1))) \quad \text{(S14)}$$

For oak,

$$deltaLAI_{max}(n) = \max(-1, \min(1, 2.66 - 0.0493 \times SWS_{index}(n-1))) \quad \text{(S15)}$$

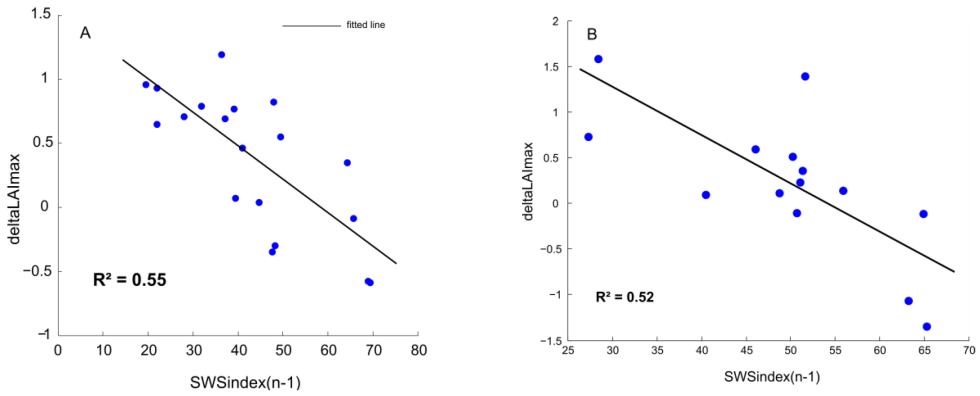

Figure S4: Dependency between deltaLAI$_{max}$ ($m^2_{leaf}.m^{-2}_{soil}$) and SWS$_{index}$(n-1) for beech (A) and oak (B).

Maximum value of LAI$_{max}$ (ageLAI$_{max}$) is determined by an envelope curve function of stand age (Fig. S5). For beech,

$$ageLAI_{max} = 9.145 - 0.038 \times age \quad \text{(S16)}$$

For oak,

$$ageLAI_{max} = 8.15 - 0.0075 \times age \quad \text{(S17)}$$

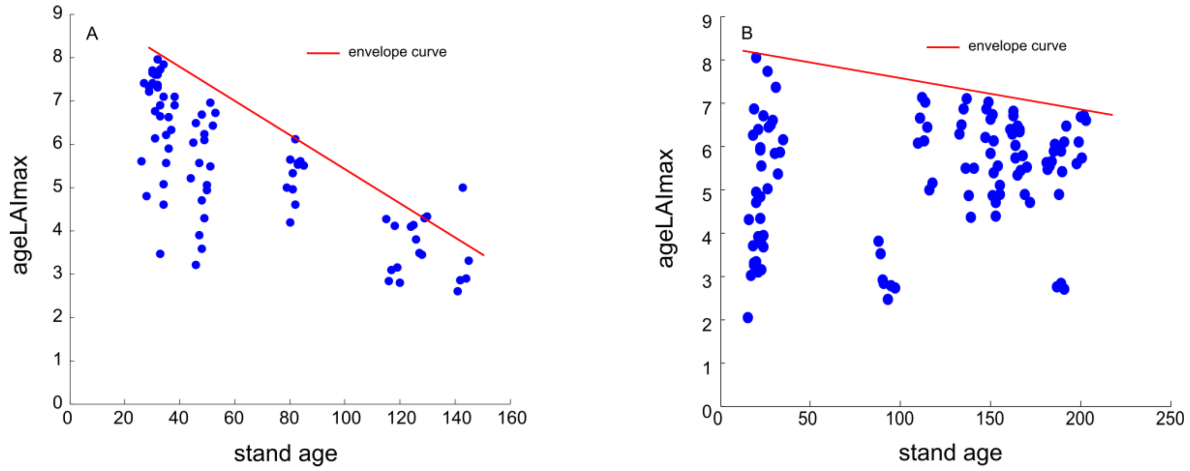

Figure S5: Evolution of ageLAI$_{max}$ ($m^2_{leaf}.m^{-2}_{soil}$) with stand age for beech (A) and oak (B).

Finally,

$$LAI_{max}(y) = \min(ageLAI_{max}, LAI_{max}(y-1) + deltaLAI_{max}(y)) \quad \text{(S18)}$$

where $LAI_{max}(y)$ is the LAI_{max} value of year y. LAI dynamic is simulated daily in CASTANEA PBM (Dufrêne et al., 2005), starting at LAI = 0 during winter, then increasing until LAI_{max} after budbreak and finally dropping to 0 after yellowing (Delpierre et al. 2009a). During leaf development, LAI increase is stopped if the carbohydrate reserve compartment is below 20 $gC.m^2$ in order to prevent carbohydrate reserves starvation. Indeed, we did not report partial or complete mortality in our study sites. Actual LAI_{max} value is consequently reduced in case of low carbohydrate reserve. In case of thinning, LAI_{max} is decreased by a reduction factor: a new LAI_{max} is calculated (Fig. S6).

$$LAI_{thin} = LAI_{max}/(a_{lai} + b_{lai}.100\tau_h) \quad \text{(S19)}$$

where LAI_{maxn} and LAI_{thinn} are the potential stand LAI_{max} and the actual stand LAI_{max} after thinning, respectively. a_{lai} and b_{lai} are parameters and h is the thinning intensity (%, see main text).

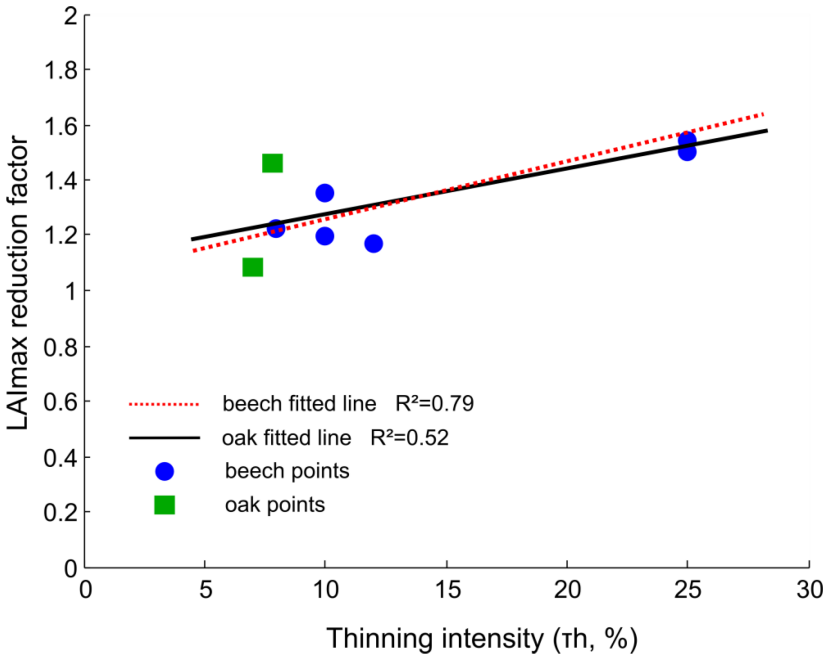

Figure S6: Thinning effect on LAI_{max}. Oak relationship has been fitted on both beech and oak points, beech relationship has been fitted on beech points only.

5.7 CASTANEA: inter-annual variation of wood growth

C allocation to wood growth is annually determined by potential allocation coefficients determined by stand age.

$$deltaSWS_{index}(n) = pdiff\,1 + \frac{pdiff\,2}{1+\exp(pdiff\,3\times(SWS_{index}(n-1) - pdiff\,4))} \tag{S20}$$

where PAC_{wood} is potential allocation coefficient to wood, age is the age of the stand, page1-2 are parameters. PAC_{wood} is then reduced by $deltaSWS_{index}$ in case of high previous year SWS_{index}.

$$deltaSWS_{index}(n) = pdiff\,1 + \frac{pdiff\,2}{1+\exp(pdiff\,3\times(SWS_{index}(n-1) - pdiff\,4))} \tag{S21}$$

$$AC_{wood}(n) = PAC_{wood}(n) + deltaSWS_{index}(n) \tag{S22}$$

Where $AC_{wood}(n)$ is the C allocation coefficient to wood in a year n, pdiff1-4 are parameters. Additionally, water stress of the current year is taking into account daily through a reduction factor flim (consequently the actual daily C allocation coefficient is $AC_{wood}(n)$ * flim).

$$flim_t = \min(1, \max(0, plim1 \times REW_t + plim2)) \tag{S23}$$

with

$$REW_t = \frac{SWC_t - SWCwilt}{SWC_{fc} - SWCwilt} \tag{S24}$$

where $flim_t$ is the reduction factor of a day t (unitless), REW_t is the relative extractable water of a day t (mm) and plim1-2 are parameters.

Parameter	Oak	Beech
page1	0.74	0.72
page2	-0.00228	-0.00264
pdiff1	-0.014	-0.01
pdiff2	-0.09	-0.15
pdiff3	-0.24	-0.4
pdiff4	60	60
plim1	7.9	7
plim2	-0.54	-0.9

Table S4: Parameterization of the wood C allocation module.

5.8 CASTANEA: species-specific parametrization

The parameterization of the CASTANEA biomass allocation module is described in dedicated sections. Other species-specific parameters are fully described in previous publications (Davi et al., 2005; Dufrêne et al., 2005; Le Maire et al., 2005). We reproduced in table S5 fundamental C balance parameters.

Description	Units	Species		Reference
		beech	oak	
Maximum sunlit leaf mass per area	$g_{dm}\ m^{-2}$	102	117	E. Dufrêne, CNRS, *unpubl. res.*
Branch nitrogen content	$mg_N\ g_{dm}^{-1}$	3.2	3.8	Ceschia et al. (2002) Barbaroux (2002)
Trunk and coarse roots nitrogen content	$mg_N\ g_{dm}^{-1}$	1.6	1.9	Ceschia et al. (2002) Le Maire (2005)
Fine roots nitrogen content	$mg_N\ g_{dm}^{-1}$	9.9	9.9	Van Praag et al. (1988)
Nitrogen dependency of maintenance respiration coefficient for stem	$mol_{CO2}\ mg_{dm}\ g_C^{-1}\ g_N^{-1}\ h^{-1}$	0.65	0.2	Le Maire (2005) D. Berveiller, CNRS, *unpubl. res.*
Nitrogen dependency of maintenance respiration coefficient for branches	$mol_{CO2}\ mg_{dm}\ g_C^{-1}\ g_N^{-1}\ h^{-1}$	0.65	0.4	Le Maire (2005)
Nitrogen dependency of maintenance respiration coefficient for fine roots	$mol_{CO2}\ mg_{dm}\ g_C^{-1}\ g_N^{-1}\ h^{-1}$	0.86	0.86	Le Maire (2005)
Nitrogen dependency of maintenance respiration coefficient for leaf	$mol_{CO2}\ mg_{dm}\ g_C^{-1}\ g_N^{-1}\ h^{-1}$	1.4	1.4	Mitchell et al. (1999)
Growth respiration coefficient for stem	$g_C\ g_{C\ organ}^{-1}$	1.38	1.38	Damesin et al. (2002)
Growth respiration coefficient for branches	$g_C\ g_{C\ organ}^{-1}$	1.38	1.38	Damesin et al. (2002)
Growth respiration coefficient for fine roots	$g_C\ g_{C\ organ}^{-1}$	1.28	1.28	Ågren and Axelsson (1980)
Growth respiration coefficient for leaf	$g_C\ g_{C\ organ}^{-1}$	1.2	1.2	Niinemets (1999)
Ratio between *V*Cmax and *V*Jmax	*Unitless*	2.2	2.1	Liozon et al. (2000) Kattge et al. (2009)
Dependency between VCmax and leaf nitrogen density	$\mu mol_{CO2}\ g_N^{-1}\ s^{-1}$	30	30.8	Liozon et al. (2000) Kattge et al. (2009)
Slope of the Ball relationship (maximum value)	*Unitless*	11.8	9.5	Medlyn et al. (2001)
Fine roots turn-over	day^{-1}	0.00006	0.00007	Bauhus and Bartsch (1996)

Table S5: Species-specific parameters involved in CASTANEA carbon balance.

5.9 Description of the RENECOFOR sites characteristics

ID	X (km)	Y (km)	sp.	Elev. (m)	Slp (%)	Exp.	Age	SWC (mm)	LNC ($mg.gDM^{-1}$)	H (m)	LAI	surveys
HET 02	657.6	2467.8	*F*	145	0	-	54	200	25	29.7	6.5	4
HET 03	651	2132.7	*F*	590	15	N	87	155	28.3	29	6.6	5
HET 09	513.7	1770.3	*F*	1250	32	SW	152	110	26.3	21.8	4.6	4
HET 14	367	2469.6	*F*	90	0	-	83	83	25.3	25.7	6.2	2
HET 21	788.5	2315.6	*F*	400	3	NE	128	80	23.5	28.6	4.3	3
HET 25	898.5	2251	*F*	570	2	W	41	110	23.6	20.1	5.5	4
HET 29	160.1	2331.7	*F*	50	0	-	64	80	24.7	24.1	5.8	2
HET 52	804.8	2314.2	*F*	440	0	-	106	100	25.2	30.2	5.9	3
HET 55	794.6	2466.9	*F*	250	0	-	88	150	25.8	29.4	5.9	4
HET 60	639.2	2480.8	*F*	138	0	--	62	160	26.6	26.8	6.6	2
HET 64	355.9	1798.7	*F*	400	44	NW	67	137	26	28.8	5.3	5
HET 76	527	2524.2	*F*	210	0	-	87	90	24.5	29.9	6.5	5
HET 81	587	1823	*F*	700	0	-	108	140	28.1	30.3	6.3	5
HET 88	891.1	2352.3	*F*	400	3	W	68	100	27.5	25.4	5.9	5
CPS 77	628.1	2383.9	*Qp*	80	0	-	113	150	24.3	27.8	6.1	3
CHP 55	850.9	2452.5	*Qr*	220	0	-	100	150	23.9	20.1	5.9	4
CHP 65	406.6	1802.9	*Qr*	370	12	SE	54	160	25.5	24.9	4.7	4
CHS 01	824	2134.1	*Qp*	260	0	-	88	170	23.7	25.9	6.5	3
CHS 03	629.8	2185.3	*Qp*	260	0	-	115	100	27.4	30.5	5.6	3
CHS 10	757.5	2368.6	*Qp*	160	0	-	83	200	22.9	24.9	6.3	3
CHS 18	583.9	2250.5	*Qp*	176	0	-	78	150	26.3	28.2	5.9	3
CHS 27	539.4	2485.6	*Qp*	175	0	-	55	170	27.2	23.4	6.5	3
CHS 35	312.1	2360.2	*Qp*	80	0	-	101	120	26.3	29.3	6.1	3
CHS 41	518.9	2286	*Qp*	127	0	-	92	180	25.6	28.1	5.9	5
CHS 51	791.9	2451.5	*Qp*	180	2	S	139	80	25.4	25.2	5.9	2
CHS 57	904.2	2438.2	*Qp*	320	15	NW	128	140	20.9	28.7	5	4
CHS 60	597.2	2488.8	*Qp*	55	0	-	60	140	26.5	25.3	6.5	3
CHS 61	477.5	2392.8	*Qp*	220	5	SE	88	110	25.8	26.9	6.7	2
CHS 68	984.9	2311.7	*Qp*	256	0	-	137	80	27.9	22	5.6	2
CHS 72	453.4	2312.5	*Qp*	170	0	-	64	170	22	24.1	5.9	4
CHS 81	552.8	1893.9	*Qp*	300	18	SE	98	100	22.1	27.8	5.3	3
CHS 88	876.1	2342.8	*Qp*	330	0	-	129	200	24.8	26.4	5.7	4

Table S6: Description of the RENECOFOR sites. X and Y are Lambert II coordinates, sp. is species, F is Fagus sylvatica, Qp is Quercus petraea, Qr is Quercus robur, Elev. is elevation, Slp is slope, Exp. is exposure, SWC is soil water capacity, LNC is averaged leaf nitrogen content, LAI is leaf area index, H is top height measured in 1991, surveys is the available number of surveys.

5.10 Variation of the mode of competition

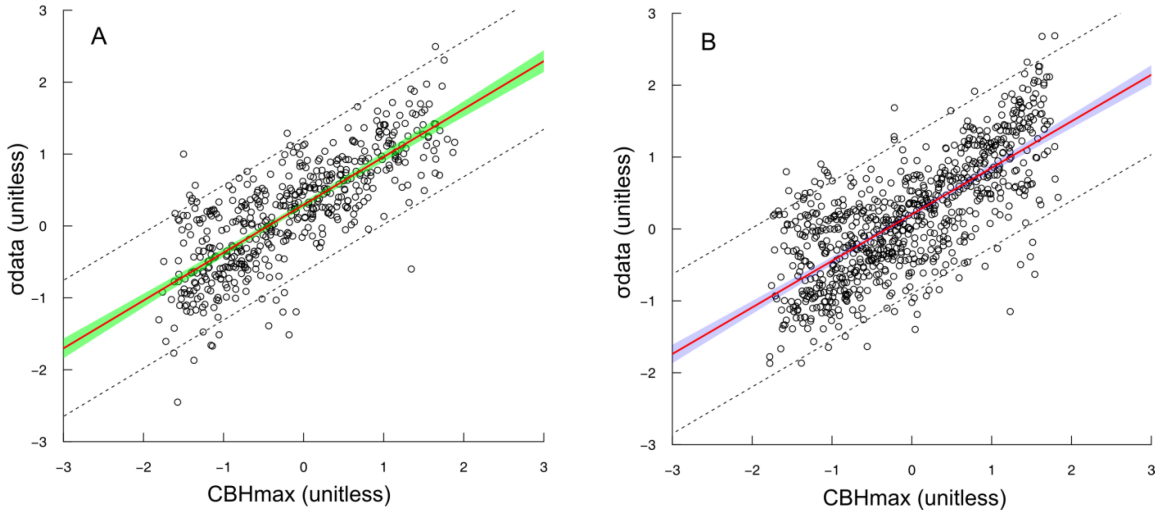

Figure S7: CBH_{max} - σ_{data} dependency at within-plot, temporal scale (within-plot standardized data, unitless) for beech (A) and oak (B). Colored areas are 95% confidence interval of the fitted regression lines.

Dependent variable	**σ**		**γ**	
Data	raw	standardized	raw	standardized
int	**<0.0001 (560.9)**	**<0.0001 (78.3)**	**<0.0001 (4205.3)**	**<0.0001 (84.5)**
species	0.88 (0.02)	0.42 (0.64)	0.93 (0.007)	0.09 (2.8)
σ	-	-	*[<0.0001 (1450.3)]*	*[<0.0001 (2089.3)]*
γ	*[<0.0001 (1456.9)]*	*[<0.0001 (2214.1)]*	-	-
Cm	**<0.0001 (169.4)**	**<0.0001 (417.3)**	*[<0.0001 (30.2)]*	*[<0.0029 (8.9)]*
SI	*[<0.0001 (31.9)]*	-	**<0.0001 (17.93)**	-
AP	*[<0.02 (5.5)]*	0.21 (1.52)	**<0.0001 (3959.3)**	**<0.0001 (4362.3)**
Species x σ	-	-	*[<0.0001 (112.6)]*	*[0.03 (4.3)]*
Species x γ	0.82 (0.04)	0.21 (1.5)	-	-
Species x Cm	0.28 (1.2)	0.97 (0.0009)	*[0.07 (3.3)]*	0.96 (0.02)
Species x SI	*[0.002 (13.6)]*	-	**0.009 (6.7)**	-
Species x AP	*[0.009 (11.1)]*	0.09 (2.8)	**0.01 (5.9)**	0.31 (1.02)
ρ	0.93	0.86	0.88	0.82
R^2	0.58	0.75	0.81	0.71

Table S7: Linear mixed model test results. Values are Pvalue (estimate). Variables retained after the bootstrap procedure are in bold. [ ] indicate variables with a Pvalue < 0.05 but not retained after the bootstrap procedure (see main text).

5.11 Goodness of fit of the individual tree growth model

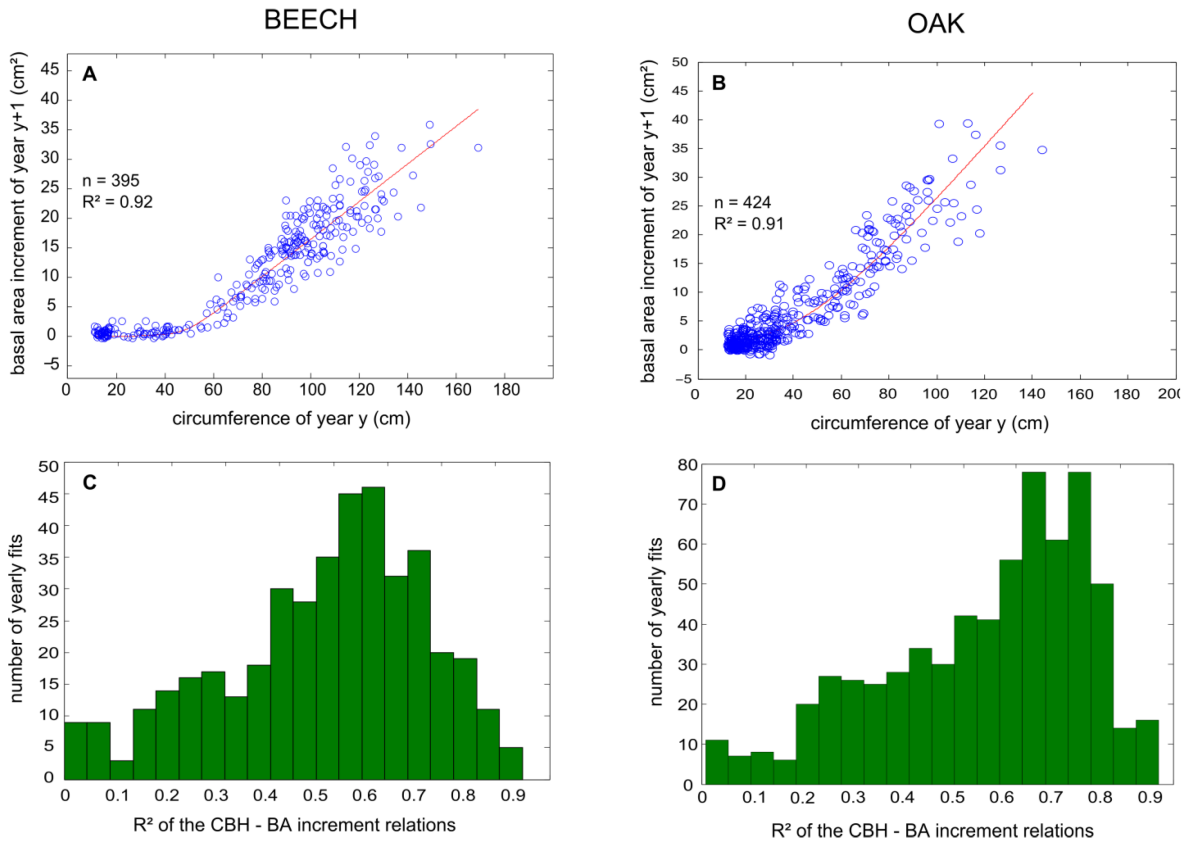

Figure S8: Illustration and goodness of fit of the individual tree growth model. A et B are based on extensive inventories lead in 2000 and 2009 in the HET03 and CPS77 plots. C and D present the goodness of fit of the model when yearly adjusted on the tree ring dataset.

5.12 Effect of contrasted thinning treatments on average annual C allocation

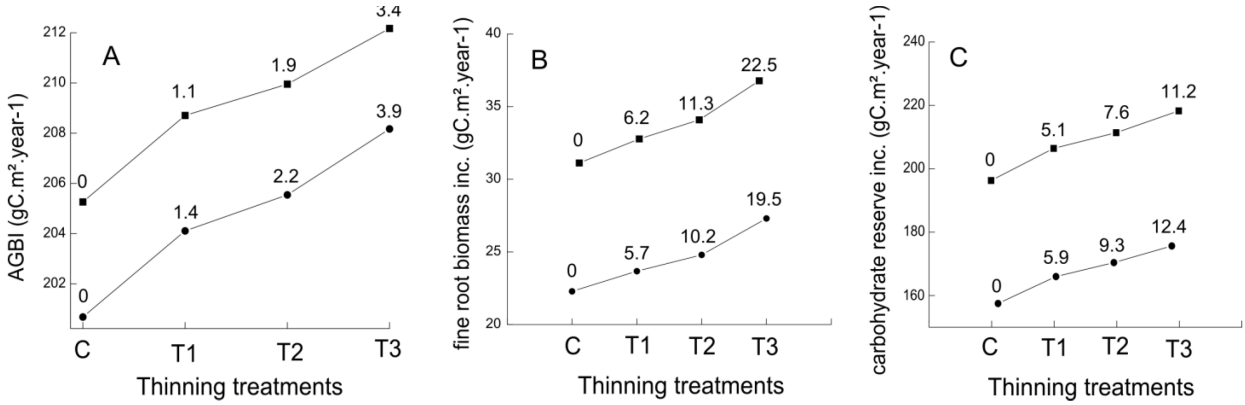

Figure S9: Effect of contrasted thinning treatments on average annual C allocation ($gC.m^2.year^{-1}$) over France for beech (circles) and oak (squares): AGBI (A), fine root biomass increment (B) and carbohydrate reserve increment (C). Treatments: C (Control treatment), T1 to T3 (Treatment with increasing thinning intensities). Figures are relative changes (%) compare to the control.

5.13 Thinning effect assessment on AGBI distribution

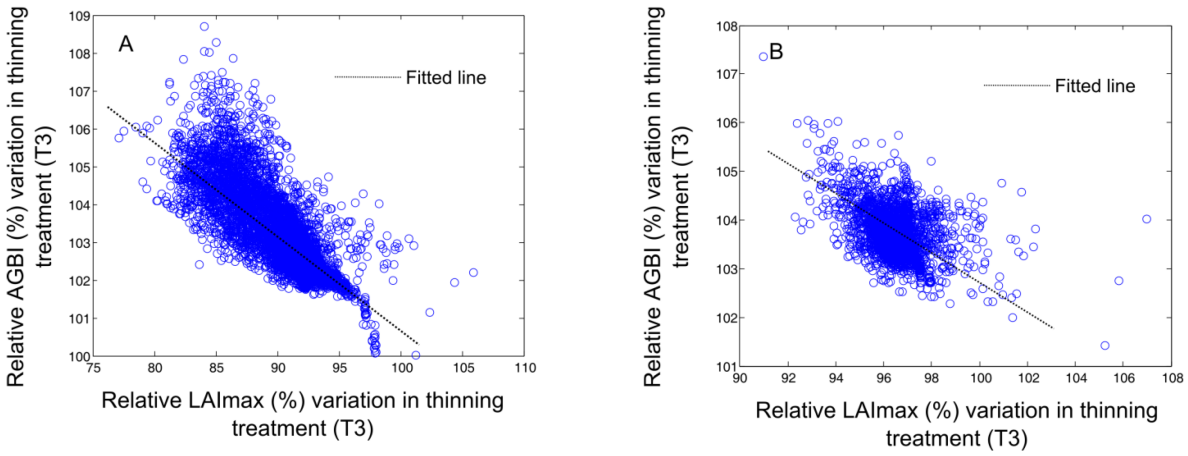

Figure S10: Relationship between the relative effects (%) of management on AGBI and LAImax in T3 compare to the control for oak (A) and beech (B).

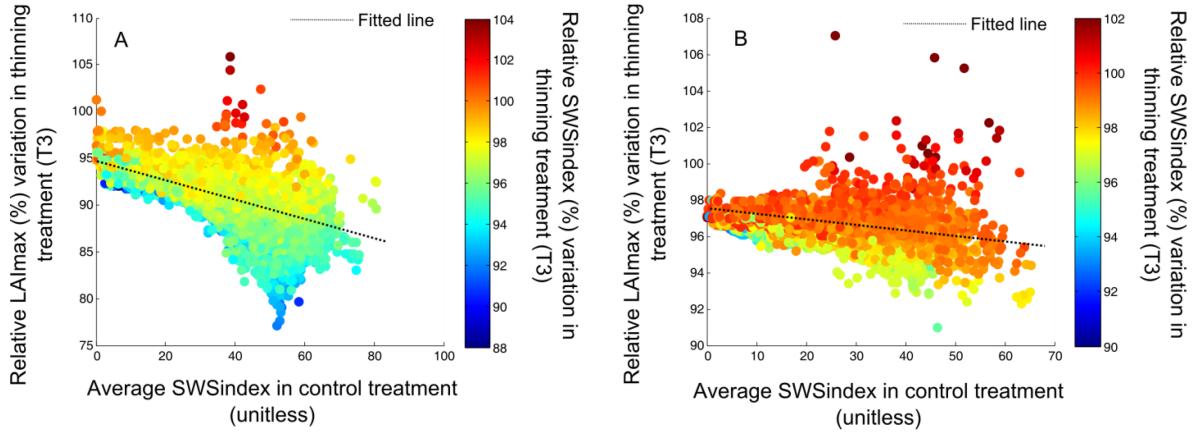

Figure S11: Grid cells distribution of the relative (%) average LAI_{max} variations over forest rotation in thinning treatment T3 compared to the control: relation with the absolute average SWS_{index} in the control. Color bar is the relative average SWS_{index} variations in T3 compared to control.

6 Afterword

6.1 Simulating the temporal evolution of size distributions

An extensive evaluation of CASTANEA-SSM should include an in-depth assessment of the ability of the model to reproduce the temporal evolution of the stand size distribution. However, the dataset used in our work is not suitable to perform this evaluation because the inventory time period is not long enough for recording significant evolution in size distribution. As an

illustration, we calculated the coefficient of variation (CV) and the skewness of the measured size distribution of all the studied plots in 1991 and 2009, along with their changes between these two dates (Table S8). It appears that the changes of these two variables are very small compare to their absolute values, and do not allow assessing the model ability to reproduce mean size distribution evolution along the stand revolution.

		Beech	Oak
Coefficient of variation	Absolute value (2009)	0.47 ± 0.21	0.62 ± 0.13
	Changes between 1991 and 2009	-0.02 ± 0.03	-0.012 ± 0.02
Skewness	Absolute value (2009)	0.18 ± 0.72	-0.32 ± 0.65
	Changes between 1991 and 2009	0.0078 ± 0.054	-0.0031 ± 0.07

Table S8: Absolute values and changes in the size distribution features over the studied plots between 1991 and 2009. Values are Mean ± Standard deviation.

We however provide here a simulation exercise (Figure S12) demonstrating that the coupled model simulates satisfactorily the general features of a tree size distribution across a forest revolution (i.e. CV and skewness decrease with mean size as observed on forest inventories, see for instance Coomes and Allen, 2007). After initializing the size distribution with a realistic CBH inventory (from HET25 plot), the simulated ranges of CV and skewness absolute values were in line with our observations on the RENECOFOR network (Figure S12, Table S8). These results are promising regarding the evaluation of CASTANEA-SSM on size distributions.

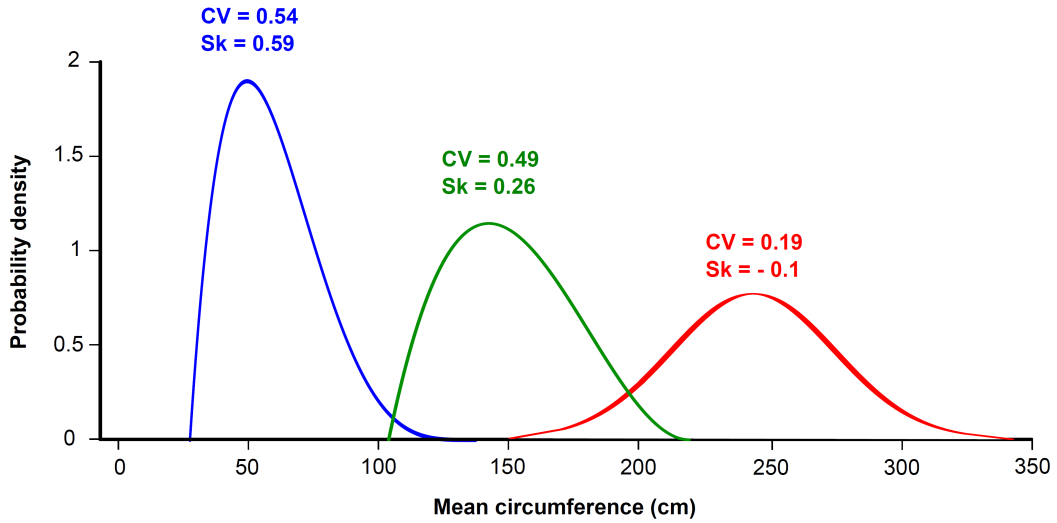

Figure S12: Simulated evolution of a stand size distribution across a forest revolution. CV: Coefficient of variation, Sk: Skewness. Initial forest inventory was generated using a beta distribution (α=2, β=5). The blue and green simulated inventories were fitted using a beta-distribution. The red distribution was fitted using a normal distribution. The adequacy of the simulated inventories with the fitted probability distributions was checked using Kolmogorov-Smirnov tests (Pvalue < 0.05).

6.2 Using the SSM with annual or pluri-annual time step: quantification of the deviation from linearity

The simulation of individual growth in the SSM and in the Fagacées model (LeMoguédec and Dhôte 2011) is mostly based on the robustness of the following equation.

$$\delta g_i = \gamma.max(ci_{130} - \sigma; 0) \qquad \sigma, \gamma \in \mathbb{R}^+ \tag{S25}$$

with δgi the individual basal area increment of the year i and ci_{130} the tree circumference at the beginning of the year i.

Measurements of individual basal area increments originate from two sources: forest inventories and tree-ring series. There is therefore an important variability in the time lag between between the two measurements necessary to obtain δg (1 year in tree-ring series, typically 3 to 12 years in forest inventories). The first publications related to the Fagacées model are indifferently based on inventory data with a 3 to 15 years time lag between two measurments (Dhôte, 1991, 1999). These data are then averaged to obtain averaged tree basal area and used along with the initial circumference in equation S25. Subsequently, the Fagacées model was used at various

time steps, notably 3 years (LeMoguédec and Dhôte 2011) and recently, 1 year in the works of Bellassen et al. (2010, 2011a).

However, we should note that if Eq. S25 is valid for δg averaged over a given period, it cannot hold true for δg averaged over different time lags. We here demonstrate this point, considering S25 true for annual δg (time lag = 1 year). In this exercice, we only study the behaviour of S25 for c>σ (i.e. δg >0), and we hypothesized that σ is a constant over the considered time period.

We defined:

- c_0, c_i, δg_i, $\overline{\delta g}$, circumference at the beginning of the considered time period, circumference at the beginning of the year i, γ value for the year i, basal area increment of the year i, averaged basal area increment over the considered time period, respectively.
- $\delta g_0 = 0$
- $A(c_0) = c_0^2 + 4\pi\gamma_1(c_0 - \sigma)$
- $$F(c_0) = \begin{cases} si\ n = 1, F_n = 0 \\ si\ n \geq 2, F_n = \gamma_n(\sqrt{A(c_0) + 4\pi \sum_{j=1}^{n-1}(F_j)} - \sigma) \end{cases}$$
- $$K(c_0) = 4\pi \sum_{k=1}^{n-1} \frac{F_k(c_0)}{c_0^2} - \sigma$$

Then, $\forall$ i $\in \mathbb{N}$

$$\delta g_i(c_i) = \gamma_i(c_i - \sigma) \qquad \sigma, \gamma_i \in \mathbb{R}^+$$

When averaging δ_g over n years, the relation $\overline{\delta_g} = f(c_0)$ can be written as follows.

$$\overline{\delta g} = \frac{1}{n} \sum_{i=1}^{n} \gamma_i(\sqrt{c_0^2 + 4\pi \sum_{k=1}^{n-1} \delta g_k(c_k)} - \sigma) \tag{S26}$$

because

$$\overline{\delta g} = \frac{1}{n}\sum_{i=1}^{n}\gamma_i(c_i - \sigma)$$

and

$$c_i^2 = c_0^2 + 4\pi\sum_{k=1}^{i}\delta g_k$$

If we introduce c_0 in Eq. S26, we obtain

$$\overline{\delta g} = \frac{1}{n}\sum_{i=1}^{n}\gamma_i(\sqrt{c_0^2 + 4\pi\sum_{k=1}^{n-1}F_k(c_0)} - \sigma)$$

$$\overline{\delta g} = \frac{1}{n}\sum_{i=1}^{n}\gamma_i(c_0\sqrt{1 + 4\pi\sum_{k=1}^{n-1}\frac{F_k(c_0)}{c_0^2}} - \sigma)$$

$$\overline{\delta g} = \frac{1}{n}\sum_{i=1}^{n}\gamma_i(c_0 * (1 + K(c_0)) - \sigma) \tag{S27}$$

The factor $K(c_0)$ therefore affects the linearity of Eq. S27. This demonstrates that the validity of Eq. S25 is hampered in the case of averaged δg.

Further,

$$\lim_{c_0\to\infty}\frac{\sqrt{A(c_0)}}{c_0^2} = 0$$

and therefore

$$\lim_{c_0 \to \infty} \frac{F_n}{c_0^2} = 0$$

$$\lim_{c_0 \to \infty} K(c_0) = 0$$

Finally,

$$\lim_{c_0 \to \infty} \overline{\delta g} = \frac{1}{n} \sum_{i=1}^{n} \gamma_i (c_0 - \sigma)$$

In conclusion, our exercice revealed that (Fig. S13):

- Eq. S25 cannot be a valid model for data averaged over different time periods
- non-linearity is maximum in the case of important annual growth
- non-linearity is maximum for c_0 close to σ and tend toward zero for high c_0
- considering Eq. S25 true for annual δ_g, non-linearity increase with the number of years averaged to obtain $\overline{\delta_g}$

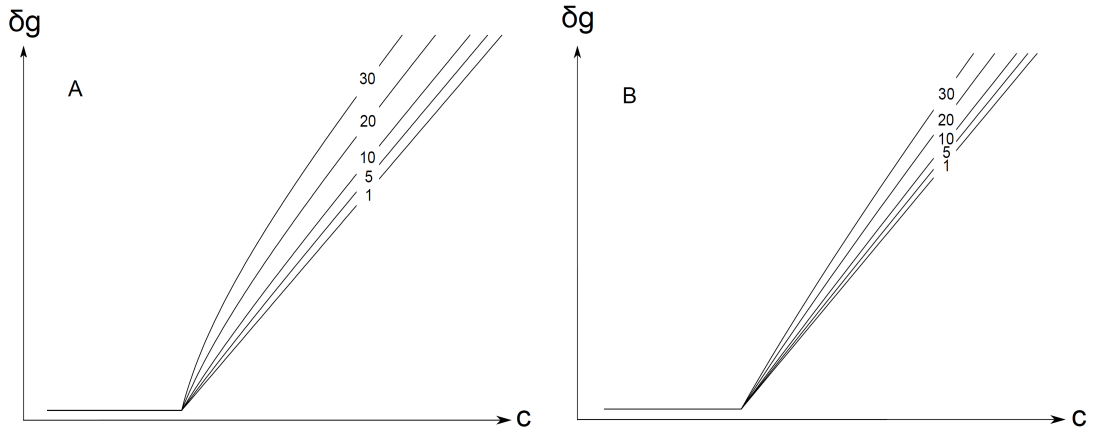

Figure S13: Graphical representation of equation S25 using data of basal area increment averaged over different time lags, considering that equation S25 is valid for annual δ_g. Figures correspond to the number of years averaged to obtain δ_g, with $\gamma = 0.6$ (A) and $\gamma = 0.2$ (B).

We considered in this chapter that Eq. S25 was valid on data averaged over 1 to 5 years (frequency of the forest inventories), following the previous publications related to the Fagacées model. Future research should bring more light on the extent to which Eq. 25 is a valid model to evaluate the size-asymmetry of competition based on growth data averaged over long time periods.

Chapter 5

General discussion and perspectives

1 Synthesis

The objective of this dissertation was to move forward our understanding of the dynamics of wood productivity and C allocation in four European forest tree species, using statistical and process-based modelling.

We characterised the dependences of annual wood growth at both stand and tree levels over France using a variety of statistical models that included linear mixed models and Random Forest machine learning (Chap. 2 and 4). We found that the inter-site variability in the fraction of C allocated to stand wood growth was predominantly driven by an age-related decline. Besides, our results supported the premise that the annual wood growth of the studied species is under a complex control including both source and sink limitations. At the tree level, we showed that annual wood growth was well predicted by the individual size. The size-asymmetry of growth, i.e., the advantage of big trees in the competition for resources, increased consistently with the whole stand productivity at both inter-site and inter-annual scales.

On the basis of our findings regarding stand wood growth dependences, we developed a new C allocation scheme in the CASTANEA model, which represent four compartments competing for C supply on a daily basis and integrate a combined source-sink limitation of wood growth (Chap. 3). The calibrated model was able to efficiently capture both the inter-annual and inter-site changes in stand wood growth that was observed across national environmental gradients. The model predictions of the C reserve pool were in fair agreement with data from the literature. In addition, CASTANEA was able to reproduce the decline of LAImax at arid sites, which we observed over France using satellite-derived data. We found that the representation of the internal and environmental factors affecting directly the cambial activity (sink limitation) was needed to predict wood growth using process-based models (PBMs). Moreover, our results indicated that the representation of the environmental control of sink activity does not affect the qualitative predictions of the future of the European forest productivity previously obtained from NPP simulations and source-driven PBMs. However, the current, source-driven generation of PBMs probably underestimates the spatial heterogeneity of the effects of climate change on forest growth that arise from sink limitations. Consequently, over the 2040-2064 period, the changes in the European wood growth predictions that were attributable to the implementation of sink limitations were comparable to the changes induced by (1) the variability of climate

associated to C emission scenario and (2) by the different assumptions about CO_2 fertilization effect on plants. Sink limitations may be of importance for the sub-regional projections of forest productivity and C sink. This calls for a more complete representation of the processes that drive forest growth in PBMs, if they are to help defining management guidelines and forest policies.

In another part of our study, we successfully used our findings regarding the dependences of annual wood growth at tree level (i.e., empirical rules of tree growth competition) to calibrate a module for the simulation of the individual size trajectory of trees in the CASTANEA PBM (Chap. 4). Our hybrid modelling approach (Fontes et al., 2010), which is grounded in both empirical and process-based concepts of wood growth dynamics, allows using our knowledge about physiological processes to help the design of new operational forest management guidelines. In turn, the coupled model was used to assess the potential effects of management on forest functioning and wood growth across France. We identified the areas where management efforts may be concentrated in order to mitigate near-future drought impact on national forest productivity. Around a quarter of the French temperate oak and beech forests are currently in zones of high vulnerability, where management could thus mitigate the influence of climate change on forest yield.

2 Limitations of our modelling approach

In this section, we discuss three important limitations of our modelling of forest productivity, with regards to the mechanistic modelling of forest growth, the modelling of tree mortality, and the modelling of nutrient cycling in forests.

2.1 Mechanistic modelling of forest growth

In this study, we mostly relied on annual growth data to improve our understanding and representation of C allocation in trees. Although we based our analyses on a PBM, that include a mechanistic representation of the processes driving water and C forest balances, our dataset thus did not allowed to conduct stringent tests on the determinism of C allocation. The principle of process-based modelling is indeed to represent the basic, biophysical processes that occur

at fine time scale and that underlie the dynamic of the studied ecosystem variable, which is considered at coarser time scale. The ability of CASTANEA to predict the daily to seasonal dynamic of tree growth remains to be evaluated in order to provide a full insight of the processes at stake. In a first attempt to discuss the processes represented in our C allocation scheme at an intra-annual scale, we show in Fig. 1 the implications of the sink limitations for the simulated intra-annual patterns of wood growth.

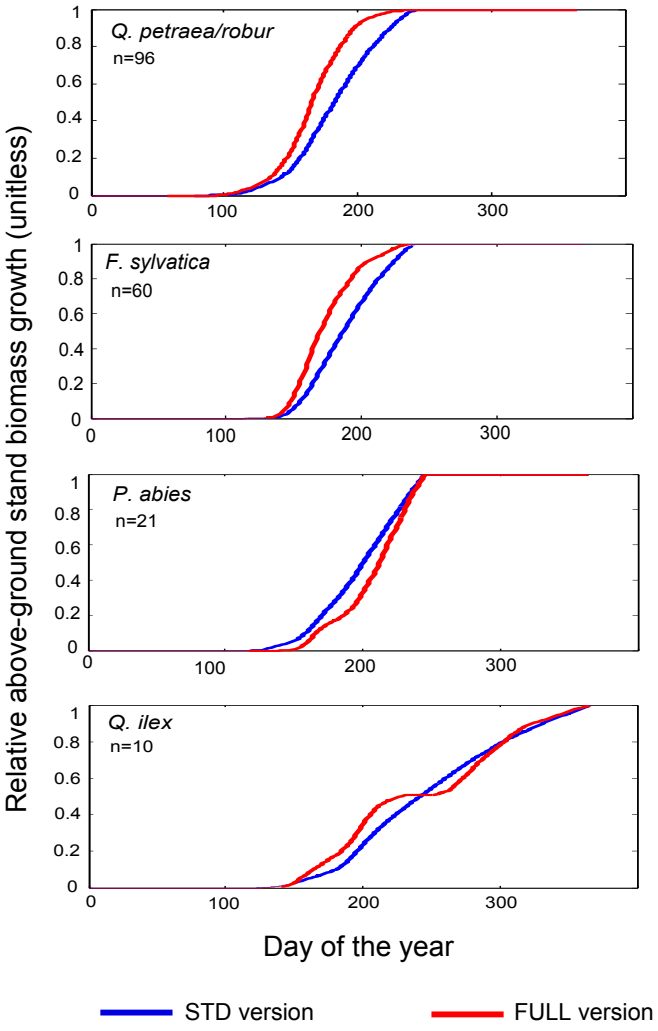

Figure 1: Comparison of the intra-annual wood growth simulated by the STD (source driven) and FULL (source-sink driven) versions of CASTANEA. This figure compares how the daily wood biomass increment is distributed over the year, when simulated with the STD or the FULL model version. For temperate oak (*Q. robur/petraea*), *F. sylvatica* and *P. abies*, the comparison has been conducted on the RENECOFOR network, across a quarter of the sites. We selected the sites with the highest effect of sink limitations on growth. For *Q. ilex*, the comparison was conducted using the Puéchabon site. All the intra-annual growth patterns have been standardized and averaged per species and per model version. For all species, the annual wood growths predicted by the STD and FULL versions were not significantly different when averaged over the studied years.

The FULL version simulated on average an earlier cessation of the wood growth period

for temperate species (*Q. robur/petraea* and *F. sylvatica*). The cessation of the period with possible C allocation to wood growth simulated with the STD version of CASTANEA is fixed to species-specific day of the year and is therefore similar in all the simulated years of growth. In the FULL version, wood growth can in addition be inhibited by the direct effect of water stress on the sink activity. This process has thus the potential to shorten the period of active growth in case of summer drought, which certainly explain the pattern observed in Fig. 1. This is in agreement with a number of studies showing that the wood growth cessation can be hasten by drought (Gruber et al., 2010; Oberhuber et al., 2014; Pichler and Oberhuber, 2007). Conversely, the FULL version predicted a delayed growth onset for *P. abies* (Boreal/Alpine species), compared to the STD version of CASTANEA. The growth resumption of trees has been showed to be strongly affected by temperature (Begum et al., 2013; Delpierre et al., 2015; Moser et al., 2010): the onset of cambium activity seems to be triggered by the warming of daily minimum air temperature in spring. In addition, Rossi et al., (2008) reported that although daily temperatures below 4-5°C are still favourable for photosynthesis, thermal conditions below these values could inhibit cambial activity and wood growth with strong implication for the wood growth phenology. This sink limitation is represented in the FULL version: the direct effect of spring low temperature on sink activity may explain the delayed wood growth onset simulated with this version. In the case of *Q. ilex* (Mediterranean species), the simulation were conducted for the Puéchabon site, where intra-annual wood growth is continuously measured using automated band dendrometers since 2004 (Lempereur et al., 2015). Intra-annual wood growth at this site shows a characteristic pattern with two periods of growth, that occur in spring and autumn, separated by a summer drought-induced cessation of growth. A recent study (Lempereur et al., 2015) revealed that the wood growth at this site is inhibited when the tree predawn water potential drops below a threshold value of -1.1 MPa, while gross primary productivity and net exchange productivity remain positive. This result indicates that the summer growth cessation is most likely induced by a negative drought effect on the sink activity rather than by a shortage of C supply. Consistently, the summer growth cessation is only predicted by the FULL version of CASTANEA (Fig. 1). Moreover, the water retention curve calculated at this site (Fig. 2) indicates that the water potential threshold for growth cessation (-1.1 MPa), corresponds to a relative extractable water value (REW) of 0.31 (unitless).

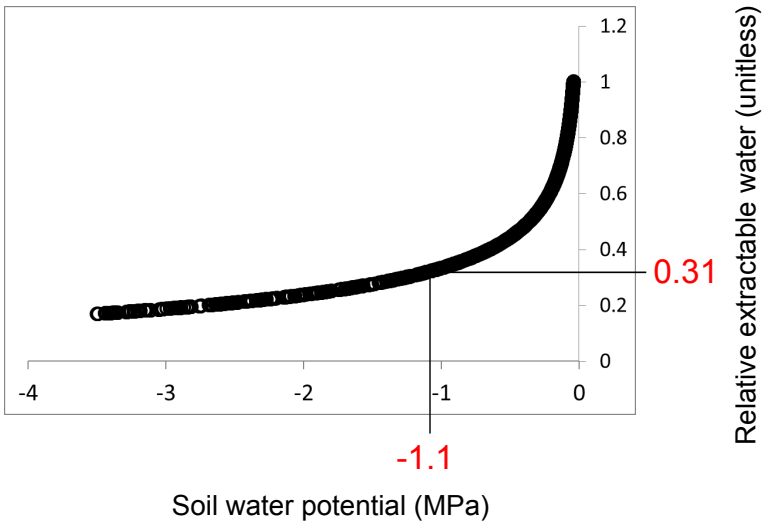

Figure 2: Water retention curve at the Puéchabon site (J.M. Ourcival; N. Martin St-Paul, unpublished result).

This REW threshold value for the drought-induced cessation of wood growth is close to the value of 0.28 that we found by calibrating our C allocation scheme using the *Q. ilex* plots of the NFI dataset (psink1 parameter, Chap. 3, Table 2).

Although the intra-annual wood growth pattern that is simulated by CASTANEA is in fair agreements with results from other studies, new developments will have to be carried out toward a mechanistic modelling of forest growth. The models that represent explicitly the meristem activities at the cell level often divide tree growth into the processes of cell division, cell enlargement and cell wall synthesis (Deleuze and Houllier, 1998; Drew et al., 2010; Hölttä et al., 2010; Schiestl-Aalto et al., 2015). These different phases are believed to be under contrasted internal and environmental controls (Babst et al., 2014; Deleuze and Houllier, 1998) that involve the effect of temperature, tree water relations and C transport among organs (Chan et al., 2015; Daudet et al., 2005; Pantin et al., 2012; De Schepper and Steppe, 2010; Steppe et al., 2006). In particular, the sink limitation of growth induced by water stress is assumed to be driven by a decrease in turgor pressure, which affects cell divisions (Hölttä et al., 2010; Woodruff and Meinzer, 2011) and is the exclusive force driving cell enlargement (Lockhart, 1965). The pressure turgor results from both the water potential of a cell and its osmotic pressure, the latter being related to the cell soluble sugar content (Cosgrove, 1981). These two - C and water related - components should thus be simulated to represent the processes underlying growth. The modelling of water potential in tree organs requires the explicit representation of the xylem water transport and plant hydraulic architecture (Deckmyn et al., 2008; Hickler et al., 2006),

that are lacking in the CASTANEA model. The osmotic pressure is determined by the quantity of soluble sugar that is actively loaded in leaf and transported to the tree organs by the phloem (Hölttä et al., 2006). A version of CASTANEA that incorporate an explicit representation of phloem transport (Eglin et al., 2010) has been published (although not used in this thesis) and will be used for further development. The sink limitation of growth induced by temperature could also be refined, for instance by using the so-called thermal time approach (Hanninen and Kramer, 2007; Schiestl-Aalto et al., 2013). Using this approach, Schiestl-Aalto et al., (2015) were able to explain the day-to-day growth variations in secondary and primary wood and needles by the temperature-driven modulation of sink activity at the SMEAR II site (Finland). They also found that the source supply was needed to explain the year-to-year growth variations, with organ-specific relationships. This confirms that the C allocation to growth depends on the environment through complex sink-source controls. Their results also emphasize that the allocation of carbon to primary and secondary wood is not necessarily synchronized, and that the specific environmental and internal controls of the growth of the different tree organs should be considered in our modelling efforts. Moreover, growth results from a complex interaction among tree organs that should be considered in a mechanistic modelling framework: the transport of assimilate in the phloem, as well as the xylem water potential, have been showed to affect the leaf stomatal conductance (Bonan et al., 2014; Nikinmaa et al., 2013; Tuzet et al., 2003); the phloem transport is affected by the xylem water potential (Sevanto, 2014); the xylem hydraulic architecture (such as the arrangement of conduits, their frequency or length) affects the tree hydraulic resistance and thus the organ water potentials (Fonti and Jansen, 2012; Fonti et al., 2010; Jansen et al., 2011); and the sink activity may regulates the leaf C assimilation (Paul and Foyer, 2001). These results pave the way for a better representation of the tree growth and within-tree C dynamic in the CASTANEA model.

2.2 Modelling of the tree mortality

Important waves of dieback have been documented worldwide in all major biomes (Allen et al., 2010). Mortality is expected to increase as a result of increasing temperature and drought, with possible important implications for the forest productivity and the terrestrial C sink (Anderegg et al., 2013; Williams et al., 2013). The current hypotheses regarding the drivers of tree mortality involve three interacting processes: C starvation, hydraulic failure and biotic

attack (Gaylord et al., 2013; McDowell and Sevanto, 2010; McDowell, 2011; McDowell et al., 2011). The mortality of a stand is simulated in the CASTANEA model if the C reserve pool equals zero. This C-centric representation of mortality (Tague et al., 2013) is crude in view of our current knowledge of tree mortality. Besides, the mortality predictions of the model have never been evaluated using datasets of mortality observations. In our projections of the future changes of wood productivity in European forests, mortality was a negligible process, occurring in less than 7% of the European area. The PBMs that incorporate the state-of-the art representation of the processes underling tree mortality simulate C starvation and hydraulic failure (McDowell et al., 2013). The integration of mechanistic pathogen models (Biesinger et al., 2000) in PBMs is an active area of research. Probably because they do not integrate biotic interactions, models usually performed better when they predict the mortality via the time spent with severe hydraulic failure and carbon starvation, rather than when they used mortality threshold (McDowell et al., 2013). The development of mechanistic models of C allocation and water relations in trees may move forward our understanding of the processes underling the drought-induced tree mortality. For instance, hydraulic failure in trees may be associated with insufficient carbohydrate content, which is required for osmoregulation (Mitchell et al., 2014; Sevanto et al., 2013); and phloem failure induced by turgor loss may promote tree mortality by affecting access to carbohydrate reserves (Sevanto, 2014).

Alternatively, empirical models of tree mortality could be used to inform PBMs regarding climatic threshold effect on forest (Adams et al., 2013; Jiang et al., 2013). Empirical models predict tree mortality using previous growth, tree size, and climate factors as predictors (Bigler and Bugmann, 2003, 2004; Williams et al., 2013). They generally perform better than PBMs in predicting observed mortality, but they do not give insight into the physiological processes involved, which question their ability to project the future forest diebacks. In any case, empirical models need long-term calibration and evaluation to ensure robust projections (Bircher et al., 2015). More generally, the collection of comprehensive mortality benchmarking datasets remains a major challenge to improve our understanding of tree mortality and improve models (Adams et al., 2013; McDowell et al., 2013). This will be achieve through international cooperative programmes (Carnicer et al., 2011; Nothdurft, 2013), collecting data from permanent plot networks, such as the RENECOFOR, which is part of the European ICP Forest Inventory (Lorenz, 1995; De Vries et al., 2003); and national forest inventories.

2.3 Modelling of the nutrient cycling in forests

It is recognized for a decade that nutrients, especially nitrogen, impose stoichiometric constraints on ecosystem productivity and may therefore reduce the potential CO_2 fertilization effect on the terrestrial C sink (Hungate et al., 2003). The progressive nitrogen limitation (PNL) hypothesis indeed postulates that increased sequestration of N in long-lived biomass or soil pools under elevated CO_2 atmospheric concentration ($[CO_2]$) causes N availability to decline and induces a negative feedback on further productivity increases in elevated $[CO_2]$ (Luo et al., 2004). Consistently, results from FACE experiments show that the initial enhancement of forest net primary productivity (NPP) and tree wood growth under elevated $[CO_2]$ often decline after 5 to 10 years (Johnson, 2006; Leuzinger et al., 2011; Norby et al., 2010). The interaction between C and N cycling has been implemented in a new generation of PBMs (e.g., Smith et al., 2014; Thornton et al., 2007; Zaehle and Friend, 2010). Although these models differ in their underlying assumptions and modelling approach, they unanimously predict lower increases of NPP and terrestrial C sink than C-centric models, especially in temperature-limited ecosystems (Zaehle and Dalmonech, 2011). Moreover, we know that other nutrients, such as phosphorus (P; Vitousek et al., 2010) and potassium (K; Manning, 2010), exert an important control on the functioning of nutrient-poor ecosystems, such as tropical forests. Recent studies suggest that the anthropic N deposition may progressively change the temperate and boreal forest productivity constraints from N to P (Jonard et al., 2015; Penuelas et al., 2013) and K (Manning, 2010; Sardans and Peñuelas, 2015) limitations. To date, only a few PBMs are able to simulate the interaction between C, N and P cycling in forests (Goll et al., 2012; Wang et al., 2010). Their first results confirm the potential importance of the P limitations on the global terrestrial C sink in the 21st century.

The version of the CASTANEA model that we used in this study does not incorporate a representation of nutrient cycling in forests. Although we explicitly considered the uncertainty associated with the CO_2 fertilization effect on forest productivity in our projections (Chap. 3), which partly account for the uncertainty associated with the future effect of nutrient cycling on forest productivity, it is an important limitation of our approach. The explicit representation of nutrient cycling may indeed reduce the overall uncertainty of our projections. Moreover, the spatial variation in the stoichiometric constraints, which may result from the spatial variation of nutrient availability (Harmens et al., 2011; Yang et al., 2013), may affect the spatial pattern of

our projections of forest productivity, with local and sub-regional implications for the forest C balance (Smith et al., 2014). The representation of nutrient cycling into the CASTANEA model is therefore a needed research avenue.

3 Perspectives

The results presented in this thesis open the way for several applications and leave a number of ecological questions unanswered.

The distribution of tree species is expected to experience important climate-driven changes in the future. PBMs can be used to project the changes in the areas potentially suitable for tree species by simulating the impact of climate change on species functioning (Jiang et al., 2013; Koca et al., 2006). Previous studies often used the simulated NPP as a proxy for suitability (Cheaib et al., 2012; Hickler et al., 2012; Keenan et al., 2011). However, wood growth may be a more reliable proxy than NPP to evaluate tree vitality (Bigler and Bugmann, 2004; Dobbertin, 2005) and fitness (Doughty et al., 2015); and a growing number of studies rely on wood growth to anticipate the outcome of climate change on forests (e.g., Benito-Garzón et al., 2013; Gaucherel et al., 2008; Gea-Izquierdo et al., 2013; Lara et al., 2013). The changes in wood growth predicted by the CASTANEA model could therefore be used to anticipate the impact of climate change on tree species ranges. In a previous study, Cheaib et al., (2012) found substantial differences between the tree ranges predicted by correlative species distribution models (SDMs), which are widely used to project changes in species distribution (Guisan and Thuiller, 2005; Thuiller et al., 2005), and the tree ranges predicted by CASTANEA. However, we recently found that using correlative SDMs in human-dominated areas, such as Western Europe, can lead to strong miss-estimations of species distributions (Appendix A3), which calls for further comparisons between modelling approaches.

The wood growth projections of CASTANEA should now be used in combination with the stand structure module presented in Chap. 4 to evaluate how management may change the responses of forests to climate change, and to help defining adaptive management guidelines for the next decades (Keenan, 2015; Schelhaas et al., 2015; Wang et al., 2012). We also need to further evaluate the uncertainty of our projections by forcing CASTANEA with different

combinations of global circulation and regional climate models. The differences in future climate change projections have indeed been reported as the major cause for uncertainty in the future forest productivity and terrestrial C sequestration (Buisson et al., 2010; Reyer et al., 2014; Zaehle et al., 2007). Finally, it is now important to combine our knowledge about forest productivity and soil functioning to quantify the implications of our findings for the projections of the future European C sink. These are promising avenues for future research.

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Evaluation of the doctoral thesis by **Joannès Guillemot**: **Productivity and carbon allocation in European forests: a process-based modelling approach**

The thesis by Joannès Guillemot is about analysing and predicting forest productivity in France, and more generally in Europe, as affected by environmental conditions and forest management. The effects of environmental conditions are treated using a process-based model (CASTANEA), and the management actions are incorporated by (1) making the growth allocation scheme of CASTANEA more sensitive to environmental and management-related stand characteristics, and by (2) coupling the model with an empirical model of stand structure development.The thesis consists of three separate, multi-authored papers led by the doctoral candidate, as well as an introduction and a synthesis. The papers contain an impressive amount of data analysis with advanced statistical methods, covering geographically extensive areas and utilising several different types of data. Model development in such a wide geographical extent is an ambitious objective, and the doctoral candidate must be congratulated for keeping it all together within a scientifically insightful and logical framework.

The objectives of the thesis are very topical in forest modelling at the moment. Several process-based models have been developed that are environment-sensitive but poor at interpreting the results on carbon fluxes in terms of stemwood growth, which interacts with forest structure in the long term. On the other hand, the empirical models that have been developed to reproduce the interactions of forest structure and stem volume growth in detail, are generally insensitive to environmental drivers. Therefore, studies to link the two approaches are in demand, and the present one is among the first to provide extensive results on such linkage.

Chapter 1 provides an insightful introduction to the topic of the thesis, up to date with references to literature. A focal topic discussed here is the decoupling of annual wood growth and annual C assimilation. This relates to the topical debate on sink and source limitations of woody growth, which has questioned the usefulness of models of C assimilation in predicting the temporal variability of woody (particularly stem volume) growth. The candidate links this particularly to the different responses of woody growth and C assimilation to water availability. Secondly, the introduction reviews the issue of forest productivity and management. Here, the focus is on competition and particularly its effects on water availability. Thirdly, simulation of C allocation and forest management by process models is reviewed. It is pointed out that predictions of different PBMs differ widely from each other, probably due to differences in C allocation, which should also take into account stand structure and management.

Chapter 2, already a published paper, focuses on the spatial and temporal variability of woody growth of four species (species groups) in France. The idea was to analyse the importance of empirical drivers of woody growth by means of a statistical analysis, where some of the explanatory variables were not direct empirical measurements but variables derived from CASTANEA simulations. GPP, in particular, was derived from the model. The forest ecosystem data came from the RENECOFOR permanent plot data base, and climate data was used to drive the process model. The study showed that while the simulated GPP was an important determinant of the

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spatial variability of the estimated woody growth, the temporal variability was also strongly controlled by sink-related factors, such as temperature and water availability. This is among the first studies (if not the first) that have shown in a large data set an important role of sink limitation in growth variability.

Chapter 3 focuses on improving the presentation of growth allocation to wood in the CASTANEA model. An empirical approach is taken, similar to that used in Chapter 2, except that now a more comperehensive allocation scheme is aimed for, instead of just looking at empirical drivers of allocation. The idea is that woody growth is simulated with CASTANEA for each location under three alternative assumptions and with a set of parameter values, the parameters are adjusted to find the best agreement with measured woody growth, and the alternative assumptions are assessed on the basis of how well they reproduce the observed patterns. Several data sources are used, including a data set on total non-structural carbon. The results indicate that a combination where the annual maximum LAI depends on soil water content and allocation to wood depends on stand age and on environmental parameters determined by current season temperature and soil water, as well as last year's soil water, fits the data best. Model parameterisation was carried out using Bayesian analysis, and the results were used for projections of forest growth during the 21st century.

Chapter 4 is a published paper that deals with combining CASTANEA with an empirical stand structure model, so as to combine the impacts of management with the process-based estimation of productivity. Again, national data are used to calibrate the combined model. The structure model accounts for the competition between trees, allowing for larger trees to have a larger relative growth rate than smaller trees. The overall growth rate is related to stand productivity. The paper demonstrates nicely that the productivity parameter, γ, correlates with site index in the empirical data and with simulated annual productivity in the modelled data. The competition parameter, σ, on the other hand is dependent on the maximum CBH of the stand, which makes sense because competition affects the trees smaller than the dominant ones. The calibrated combined model was able to reproduce a high percentage of observed variability in woody growth (assessed on the basis of basal area growth).

In Chapter 5, the author provides a critical appraisal of the results. The main issues discussed include the representation of the source-sink dynamics, tree mortality and forest management in models. I agree that these areas can be identified as the most important sources of uncertainty in current forest models. The author thoughtfully reflects the most recent literature on these topics and provides his ideas of the current shortcomings of his own work, as well as how to move forward in terms of model development. This section nicely manifests the scientific maturity of the doctoral candidate and gives promise of solving interesting and important scientific questions in the future.

While I think that the thesis as a whole is very comprehensive and impressive as well as moves the field of process-based modelling forward in many respects, I would like to add some critical notions concerning especially the representation of the interactions of tree and stand structure and woody allocation in the present approach. These comments should be taken as suggestions for developing the approach further, rather than as serious shortcomings of the thesis.

While the present results on the impact of environmental factors on woody allocation, based on within-year source-sink analysis, are quite novel, I think that another aspect of woody allocation that has been present in process-based models for a long time, has here not been discussed very clearly. This is related to the trend-like changes in allocation that follow from the change of tree size and structure. Some of the first papers on this issue were published in the 80s, including Valentine (1985) and Mäkelä (1986) (so it is not such a recent observation in growth modelling that allocation matters! - ref. comment on page 99), and the approach of those papers has been incorporated in many growth models since (e.g. 4C, LPJ, etc). Also the 3PG model has a similar

approach to allocation trends with size (Landsberg et al. 1997). Even though these schemes do not consider environmentally induced year-to-year variations in woody growth, they still pose a trend-like requirement that must be added to the annual variability. One of the consequences of these schemes is that woody allocation first increases as trees grow in height, then reduces because the maintenance costs increase so much that all growth is directed towards satisfying the demand to replace foliage and fine root turnover (Valentine 1999). This also leads to the decline of growth with age, found here "empirically", but has been found to follow from the basic assumptions in previous studies (e.g. Härkönen et al. 2010). Here the result is obviously related to the assumptions made about height growth and how height growth declines with age. Because woody growth is a function of height growth and basal area growth, the age-related decline in height growth will automatically lead to an age-dependence in allocation.

This brings me to a principal comment on the results of Chapter 2 and particularly on their interpretation. The Chapter is concerned with the temporal variability of *woody growth*, however, it is only diameter growth (circumference, CBH) that has been monitored on a temporal basis. Woody growth is derived using (1) height growth, estimated with empirical equations based on CBH, and (2) biomass growth derived with equations based on CBH and height (except for one species were only CBH is used). So the variability in woody growth is based totally on the variability of diameter growth. It can't be assumed *a priori*, however, that height growth as well as the length and diameter growth of branches would follow the same temporal drivers as diameter growth. In fact there is recent evidence of the opposite (Schiestl-Aalto et al. 2015). The author does acknowledge this in the Introduction and Discussion, however.

Another structural aspect that was not very clear in the analysis is the relationship between tree height and diameter and how this depends on stand density and tree status in the stand. Because of this, it is not possible to use a "universal" height-diameter relationship. There is also evidence that the H/D ratio is strongly related to the crown ratio of trees (crown length to total height), which in turn has an impact on growth allocation. The smaller the crown ratio, the larger the proportion of C allocated to stems and the smaller the ratio allocated to foliage and branches. Therefore, tree structure that developed in a dense stand will largely constrain the allocation of growth to foliage for some time after thinning (particularly in species that do not resprout from the stems), as the crowns are small and the bare stems growing in diameter are long. This is likely to be important for the predictions of woody growth allocation after thinning (Kantola et al. 2007).

I found it a rather curious result of the combined simulation in Chapter 4 that thinning did not seem to affect GPP but reduced R_A and hence increased NPP. As the authors mention in the discussion, thinning has not been observed to increase volume production in forest stands. On the contrary, heavy thinning usually reduces volume production (which of course is not exactly the same as above-ground woody growth). In the forests that I am most familiar with, thinning has not been observed to increase production (e.g. Mäkinen and Isomäki 2004, Zeide 2001). My understanding of what happens after thinning is that canopy GPP goes down because leaf area is reduced and at the same time, the clumping effect of canopy foliage is increased, so part of the light is not captured by the trees because of the gaps formed in thinning. This cannot be simulated if you use a horizontally homogeneous light model, but the effect of clumping has been studied with stand structure models that simulate light interception and photosynthesis (Oker-Blom et al. 1989, Nilson 1992). The clumping effect has been found to depend on the foliage to surface area ratio of crowns (Duursma and Mäkelä 2007).

Further to thinning effect on C fluxes, Vesala et al. (2005) found that after thinning, total GPP and NEE in a boreal Scots pine forest remained almost unaltered. However, there was evidence that the contribution of the understorey to the total GPP increased after thinning, while the tree canopy contribution decreased. It should be noted that eddy covariance studies do not generally provide information about the split of GPP or NEE between trees and understorey.

It is also an empirical finding in forestry that after thinning, the rise of the crown base slows down for a while, and more growth is allocated to growing the branches and foliage than the stems. This means that even if the productivity per each tree increases because more resources become available, stem volume growth does not increase as fast, because the allocation to the crown is increasing. Simultaneously, thinning usually reduces height growth relative to basal area growth, so if you assume a fixed diameter-height model, you may overestimate stem volume growth after thinning.

Inspite of the above comments and suggestions, I found the thesis very inspiring with novel results especially concerning the impacts of water limitation on woody growth. Also the combination of a process-based model with an empirically based stand structure model seems to be the way to go, as both structure and environmental impacts are crucial considerations for future forest growth. I was impressed by the utilisation of different, extensive data sources, and the way the author had it all in control. I look forward to seeing the unpublished manuscript also in print - perhaps eventually as more than one paper, because of the huge information content of Chapter 3!

In summary, I find the thesis by Joannès Guillemot to be very interesting, very topical, fully satisfying the requirements of scientific method, and generally showing the scientific insight and maturity of the author. I have therefore no hesitation in recommending that the manuscript be accepted for presentation as doctoral thesis, and I look forward to an interesting discussion during the defense.

Sincerely

Annikki Mäkelä

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À l'Ecole Doctorale SCIENCE DU VEGETAL

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Iéna, le 26 Mai 2015

Madame,

Veuillez trouver ci-joint mon rapport d'évaluation de la thèse intitulée "Etude des la productivité et d'allocation du carbone des forêts européenes: une approche basée sur la modélisation des processus", présentée par Monsieur Joannès GUILLEMOT en Doctorat Sciences du Végétal.

Le mémoire comprend cinq chapitres, y compris une introduction, trois manuscrits de style peer-review (dont deux publiées), et une chapitre de synthèse. La thèse est plutôt bien écrite et est bien structurée. Le mémoire est un document riche et remarquable, témoignant de compétence profonde dans la matière complexe de l'observation et de la modélisation des forêts. On peut regretter quelques défauts mineurs dans la présentation et la discussion de ces résultats très complexes. Le mémoire est une contribution importante dans le domaine scientifique de la modélisation de la croissance des forêts tempérées. L'ensemble de ces éléments me permet de soutenir sans réserve la demande de M. GUILLEMOT de soutenir cette thèse devant le jury de l'université Paris-Sud.

Je vous prie d'agréer, Madame, l'expression de mes salutations distinguées.

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Rapport détaillé sur la thèse "Etude des la productivité et d'allocation du carbone des forêts européenes: une approche basée sur la modélisation des processus" présentée par M Joannès GUILLEMOT.

The thesis entitled "Etude des la productivité et d'allocation du carbone des forêts européenes: une approche basée sur la modélisation des processus" presented by Joannès GUILLEMOT comprises an introductory chapter, three chapters presenting novel results in the form of peer-reviewed papers including supplementary material, a synthesis chapter, as well as a comprehensive bibliography. The thesis is generally well structured and written, with appropriate and well-designed illustrations to underline important points. Two of the scientific chapters have been published in established international journals. An annex is also provided comprising three additional publications (two accepted) to which Joannès GUILLEMOT has been contributing, demonstrating an overall advanced capacity to generate significant research output.

The thesis follows a logical path from the analysis of forest dendrochronological and inventory data to understand important regional trends in the C allocation of wood, to the further development of a stand-scale, process-based physiological forest growth model to account for the lessons learned, and to the investigation of the effects of forest demography and management on forest growth. Analysis are performed on the plot and regional to continental scale, adding to the overall scope of the thesis. I have been impressed by the breadth of the observational and modelling methodology employed in this thesis and the mostly competent way to deal with the diverging streams of information.

A central theme of the thesis deserving particular emphasis is the role of sink control processes in affecting wood growth, which is investigated both from an observational and modelling perspective. The results convincingly show and adequately discuss that there is a notable effect of cambial control on woody growth. However, they also demonstrate that this does not imply that source-driven limitation would not strongly affect wood growth. This is a very significant finding with far reaching implications for the modelling of forest growth, which is clearly discussed with all the caveats and complex interactions that typically confound nice and simple conceptual ideas on ecosystem functioning.

In detail:

- The first chapter provides a comprehensive introduction into the research area of forest growth modelling under changing environmental conditions, outlining the relevance of this topic for understanding forest management options under future climatic change. Based on this background, M GUILLEMOT develops his objectives, namely to understand regional trends in wood allocation (Chapter 2), to incorporate these findings into a process-based forest growth model (Chapter 3), to couple the forest growth models to a novel representation of forest management with the aim to make future projections of the wood productivity of European forests (Chapter 4). This is followed by a fairly concise description of the methods and observations used for this thesis. The final section outlines the remainder of the thesis. At this place it would have been appropriate to clarify the contribution that M GUILLEMOT has made to the subsequent three Chapters, all of which are multi-author papers, first authored by M GUILLEMOT.

- The second chapter analyses observations from a forest growth monitoring network (dendrochronology and inventory) with respect to the question whether the wood growth in forest was determined by source (photosynthesis) or sink (cambial) processes. This statistical analysis of observations (aided suitably by modelling to close observational gaps) shows that there is a strong age-related decline in wood allocation, and that, at the interannual time-scale, variability in tree growth is not only driven by source (photosynthesis) variability. This leads M GUILLEMOT to conclude that sink related processes also play an important role. Based on these findings, a conceptual framework is laid out and then used in Chapter 3. The strength of this chapter is the combination of different data streams to tackle a highly relevant research question, which is otherwise based on tissue-level studies or even less direct field-based evidence. While I do not think that this study settles the question fully, it is a major advance to shed light into the question of whether sink or source processes control growth in the field and at longer time-scales. I have been the editor of this manuscript for Biogeosciences, and can report that both reviewers suggested only fairly minor revisions to the first submission, to which M GUILLEMOT responded timely, clearly and adequately.

- The third chapter (as yet unpublished) introduces a novel wood allocation scheme that not only accounts for the observed decline in wood allocation, but also embraces the concept of a balanced source-sink limitation of growth. This is probably the most innovative chapter of the thesis. The outcome of this study is that sink limitation clearly affects forest growth, without overriding the effects of source control - this is a highly significant finding. The FULL model including age related decline and sink limitation reproduces best observed patterns in forest growth. The FULL model also has 6 more parameters than the intermediate model with age-related decline (STD), raising the question whether the improved fit is merely a result of overparameterisation. Subsequent careful analyses refute this idea - to the extend possible. In a veritable tour de force the model is then applied for a range of future climate and CO2 change scenarios, which demonstrate that sink limitation as implemented here affects future trajectories of wood growth, but does not override trends imposed by the source control of growth. To maintain focus, it may be advisable to split the chapter into two papers for peer-review. The chapter has a range of smaller issues, which I detail here:
  - The introduction (and partly the discussion) overstates the relevance of sink limitation somewhat. Faitichi have claimed the current generation of models ignoring sink limitation would be "getting things right for wrong reasons" without any proof, and statements like these should not be repeated bluntly and interpreted with great care. This is particular the case, as the results presented here offer a much more balanced view in that they clearly demonstrate that sink control affects forest growth (I don't think that anyone ever said it would not - it is a question of time-scale and magnitude, and whether in the long run, one can simulate forest growth without), but that the predominant effects in terms of future responses are still driven by changes in source control. I believe that the manuscript could be benefit from being phrased more as a way to reconciling conflicting views.
  - Different to the rest of the thesis, the term terrestrial biosphere modelling is used to refer to the more general class of process-based models. This is inadequate, because the model is question only represents European forest species, and not the whole (or

at least a significant proportion of) terrestrial biosphere. The term process-based model would be more appropriate.

- In the model description, it would have been helpful to write down the C allocation equation of the full model, to appreciate better the fraction of wood C allocation. Also, the factors introduced with eq 3-6 could have deserved somewhat more of a justification. Finally, eq 5 contains a redundant term "pwood3", which is apparently never used in the model fitting, as no results are reported (and it anyway collapses with pwood1). I remain wondering what happens to the C if sink limitation stops growth completely. Will the storage term increase infinitely, will this reduce photosynthesis, or increase respiration? Assuming a parameterised stop-date for growth is a severe impediment for applying the model at the European scale.
- I did not find a reference to Table 3 in the text, nor a reference from Table 3 to the Appendix, in which the uncertainty of the parameter estimates is adequately described and presented. It would be helpful to include an estimate of the confidence range for each parameter in Table 3 to gauge the confidence to be placed in the model calibration, and the within species differences of the parameters.
- Does Figure 7 still mix spatial and temporal variability? How much of the correlation shown is due to inter-site variations rather than interannual variations?

- The fourth chapter is a published peer-reviewed article developing, evaluating and applying a new stand structural model including a generic forest management. The model and its evaluation are clearly described and demonstrate that the resultant model simulations agree within reason with observations, lending confidence to the model's prediction of woody biomass growth. The impact of thinning is clearly evaluated at the stand and regional scale and adequately discussed. This chapter also includes a substantial Appendix detailing the model implementation and supplementary data used for the study, demonstrating the high investment of work into the development of this chapter. In particular, I have appreciated the epilogue, which highlights the lack of an evaluation of the temporal dynamics of the model, offering nonetheless some hints as to the general acceptability of the results.

- The synthesis chapter briefly summarises the major findings of the thesis and then outlines a number of caveats and future research directions, with which to overcome these. These concern mainly the improved representation of the processes controlling sink limitation, mortality and nutrient constraints. I would have appreciated if one would have linked the question of sink and nutrient limitation, as opposed to thinking of nutrient limitation mostly as a factor affecting the source limitation of forest growth - but this is a minor point.

In conclusion, the author demonstrates profound insight into the topic and high level of competence in the processing, development and analysis of observational and modelling information. All three scientific chapters contain substantial novel ideas and output that are clearly a relevant contribution to the scientific understanding of the controls of forest growth. Based on the above, I recommend without any reservation that the thesis is accepted for presentation and defence in front of the respective university committee.

Université PARIS-SUD 11

FACULTÉ DES SCIENCES D'ORSAY

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Etudiant : M. JOANNÈS GUILLEMOT né le : 14/05/1987

Diplôme : DOCTORAT BIOLOGIE

Titre des travaux : PRODUCTIVITY AND CARBON ALLOCATION IN EUROPEAN FORESTS : A PROCESS-BASED MODELING APPROACH.

Ecole doctorale : Sciences du végétal : du gène à l'écosystème

Directeur : M. ERIC DUFRÊNE

Codirecteur : M. NICOLAS DELPIERRE

Lieu de soutenance : SALLE DE CONFERENCE BATIMENT 362 UNIVERSITE PARIS SUD 91 ORSAY

La soutenance est publique.

Résultat : très favorable -

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Avis de reproduction : oui.

Membres du Jury

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M. NICOLAS DELPIERRE	Docteur	UPSUD	co-directeur	
M. ERIC DUFRÊNE	Directeur de Recherche	CNRS	co-directeur	
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Mme ANNIKKI MÄKELÄ	Docteur	Univ. Helsinki	rapporteur	
M. SÖNKE ZAEHLE	Docteur	Max Planck Inst.	rapporteur	

Pour le Président et par Délégation

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LE RAPPORT DE SOUTENANCE établi par le Président du jury Doit être rédigé au verso de ce document.

Les diplômes de Doctorat délivrés par Paris-Sud ne comportent désormais plus aucune mention. (décision du Conseil d'Administration du 17/12/2012)

Rapport de soutenance

Français:

Lors d'une présentation très claire et très structurée, Joannès Guillemot a exposé de façon pédagogique et synthétique ses travaux de thèse. Il a réussi à illustrer simplement, étape par étape, des démarches complexes d'analyse d'importants jeux de données et de modélisation. L'ensemble de son exposé a mis en exergue les résultats clés et leur originalité. Joannès Guillemot a également donné des éclairages complémentaires à son manuscrit répondant aux interrogations émises dans les rapports écrits. La discussion était de haut niveau scientifique et a suscité d'intéressants débats. Avec un esprit vif, Joannès Guillemot a répondu aux questions posées de manière enthousiaste, faisant preuve de la maîtrise d'une large palette de domaines (des aspects sylviculture aux processus en écologie), d'outils statistiques et d'échelles d'étude (continentales, régionales, peuplement jusqu'à des échelles fines physiologiques). Il s'appuie aussi sur une très bonne connaissance des travaux antérieurs et de la bibliographie scientifique. Ses réponses ont témoigné de sa grande maturité scientifique et de son honnêteté notamment quant aux limites actuelles du modèle utilisé et développé. Les membres du jury ont unanimement félicité Joannès Guillemot pour l'excellence de ses travaux, leur valorisation scientifique (5 articles dont 2 en premier auteur) ainsi que pour la qualité de la présentation orale et de la discussion, menées de plus en anglais.

English version:

In a very clear and structured presentation, Joannès Guillemot presented his thesis work in a pedagogic and synthetic manner. He managed to illustrate in simple steps the statistical procedures necessary to analyse the large data base used, as well as the complex modeling studies. His presentation highlighted key results and their originality. In responding clearly to queries of the written reports, Joannès Guillemot also provided additional insight into his manuscript. The discussion following the presentation was of a high scientific level and stimulated interesting debates. Quickly thinking, Joannès Guillemot answered questions enthusiastically, demonstrating substantial knowledge in a wide range of areas (forestry aspects to ecology process), statistical tools, and scales of study (continental, regional, stand, to fine physiological scales). His answers demonstrated a firm knowledge of previous works and the relevant scientific bibliography. His answers gave evidence of his scientific maturity and honesty in particular regarding the current limitations of the applied model concepts. The jury members unanimously congratulate Joannès Guillemot for the excellence of his work, as well as for the quality of the oral presentation and discussion, which were notably conducted in English.

SUMMARY

The processes that underlie forest productivity and C allocation dynamics in trees are still poorly understood. Forest growth has for long been thought to be C limited, through a hypothesized causal link between C supply and growth (source control). This C-centric paradigm underlies most of the C allocation rules formalized in process-based models (PBMs). However, the source limitation of growth has been questioned by several authors, arguing that meristem activities are more sensitive than C assimilation to environmental stresses (e.g., water deficit and low temperatures). Moreover, the effect of management, which strongly affects forest functioning and wood growth, is not accounted for in most of the PBMs used to project the future terrestrial C sink. Our main objective in this thesis was to move forward into our understanding of the constraints that affect - or will affect - the wood productivity in European forests, from present to the end of the 21st century. We addressed this objective through the improvement of the representation of the forest productivity and C allocation in the CASTANEA PBM, building on a detailed analysis of the key drivers of annual wood productivity in French forests over the last 30 years.

Our results supported the premise that the annual wood growth of the studied species is under a complex control including both source and sink limitations. The inter-site variability in the fraction of C allocated to stand wood growth was predominantly driven by an age-related decline. At the tree level, we showed that annual wood growth was well predicted by the individual size. The size-asymmetry of growth, i.e., the advantage of big trees in the competition for resources, increased consistently with the whole stand productivity at both inter-site and inter-annual scales. On the basis of our findings, we developed a new C allocation scheme in the CASTANEA PBM, which integrate a combined source-sink limitation of wood growth. The new calibrated model captured both the inter-annual and inter-site changes in stand wood growth that was observed across national environmental gradients. The model was also successfully evaluated against a meta-analysis of carbohydrate reserve pools in trees and satellite-derived leaf area index estimates. Our results indicated that the representation of the environmental control of sink activity does not affect the qualitative predictions of the future of the European forest productivity previously obtained from source-driven PBMs. However, the current, source-driven generation of PBMs probably underestimates the spatial heterogeneity of the effects of climate change on forest growth that arise from sink limitations.

Further, we successfully used our findings regarding the dependences of annual wood growth at tree level (i.e., empirical rules of tree growth competition) to calibrate a module for the simulation of the individual growth of trees in the CASTANEA model. The coupled model was used to assess the potential effects of management on forest functioning and wood growth across France. We identified the areas where management efforts may be concentrated in order to mitigate near-future drought impact on national forest productivity. Around a quarter of the French temperate oak and beech forests are currently in zones of high vulnerability, where management could thus mitigate the influence of climate change on forest yield.